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VOLUME 8

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BIOLOGICAL STUDIES OF ECONOMIC SIGNIFICANCE OF THE YELLOW-EYE MULLET, *ALDRICHETTA FORSTERI* (CUVIER & VALENCIENNES) (MUGILIDAE)

By J. M. Thomson*

[*Manuscript received August* 1, 1956]

Summary

This species attains a relatively small size (40 cm maximum) and an age of 7 years. The smallest fish recorded with mature gonads were 22 cm length to caudal fork (male) and 24·5 cm (female). The species matures at the end of the third year. Two races are distinguishable, a summer-spawning group in Victoria and Tasmania and a winter-spawning group in Western Australia. Fecundity varies from 125,000 eggs in a female 24·5 cm long to 630,000 in one 39·1 cm long. The condition factor increases markedly in fish with ripening gonads.

In Western Australia only 3·3 per cent. of yellow-eye mullet in market samples were less than the legal minimum size. Mesh tests show that 2¼ in. mesh is sufficient to permit escape of undersized fish.

The species feeds on any small organic material, plant, animal, or detrital.

Existing management policies are effective in maintaining stocks.

I. Introduction

During 1947 and 1948 the author was engaged on research on the sea mullet, *Mugil cephalus* Linnaeus, in Western Australia. The opportunity was taken to make observations on the yellow-eye mullet, *Aldrichetta forsteri* (Cuvier & Valenciennes), which is frequently taken in the catches with the sea mullet. Some earlier data are also available from south-eastern Australia. In several respects the data are not complete; but as it appears unlikely that an opportunity to further these studies will eventuate, the knowledge gleaned is presented here for the information both of those interested in the management of the stocks of this species and of those who are interested in the biology of Australian fish. Certain data on feeding (Thomson 1954*b*) and on linear growth (Thomson 1957) have been reported upon elsewhere and will not be repeated here except where relevant to the discussion.

II. Range and Distribution

The species ranges from the Murchison River, W.A., in the west to the Hawkesbury River, N.S.W., in the east. However, it is taken in commercially important numbers only south of Geraldton, W.A., and south of the New South Wales–Victorian border. It is taken both in estuaries and on the sea beaches. As far as is known it does not venture far away from the coast. This species also occurs in New Zealand (Phillipps 1921, 1927; Thomson 1954*a*).

* Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, N.S.W.

III. Form and Growth

A general description and the relative proportions of the parts of the body have been given by Thomson (1954*a*, Table 3 and p. 115). That the linear proportions of the body remain constant, at least after a length of 6 cm is attained, is shown in Figure 1, where the regression lines of length to the caudal fork (L.C.F.), anal length (A.L.), and head length (H.L.) on total length (T.L.) are straight.

A length-weight relationship of normal type is demonstrated in Figure 2. In early life there is a fairly low ratio of weight to length, but during the third year when the fish is maturing there is a rapid increase in relative weight; and after maturity is reached, weight increases at a constant rate relative to length during the remainder of life.

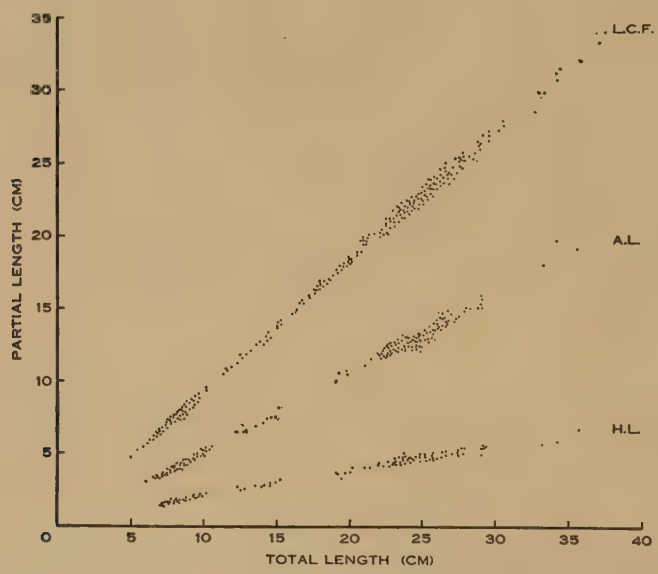

Fig. 1.—Relationship between total length and linear measurements of the body.

Figure 2 combines samples taken at all times of the year. There are, however, seasonal fluctuations in weight, as is best demonstrated by the condition factor K derived from the relationship $K = W/0{\cdot}01L^3$, where W is the weight in grams and L the length in centimetres. The seasonal variation in K is illustrated in Figure 3, which shows only a slight variation in immature fish but marked increase in relative weight in maturing fish.

IV. Size Distribution

The mean size of yellow-eye mullet in the estuaries of the south coast of Western Australia seems to be larger than that on the west coast (Table 1). The modal size group in the commercial catch of the western estuaries is generally at or about the legal minimum total length, which is 9 in., equivalent to 22·9 cm T.L. or

20·0 cm L.C.F., the last being the measurement preferred in scientific work as being more accurate (Table 1).

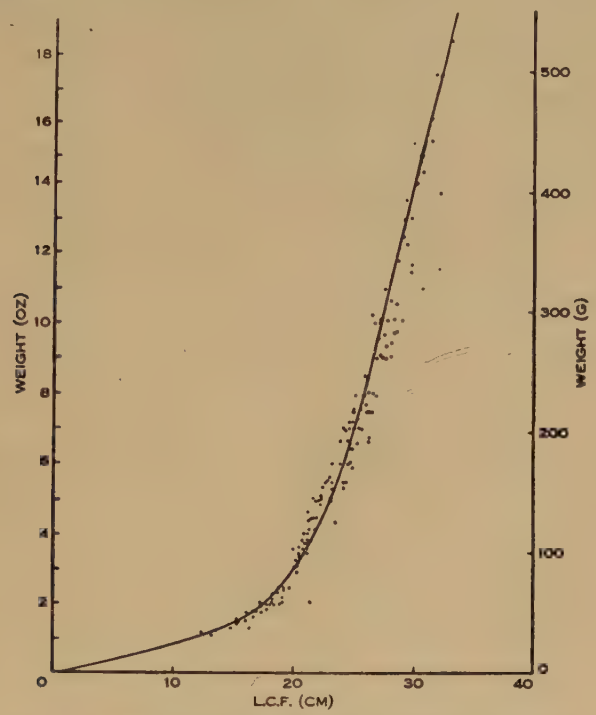

Fig. 2.—Length-weight relationship of yellow-eye mullet.

Less complete data for the other rivers on both coasts confirm this picture. The difference is not due to any local variation in net mesh, for in our experimental

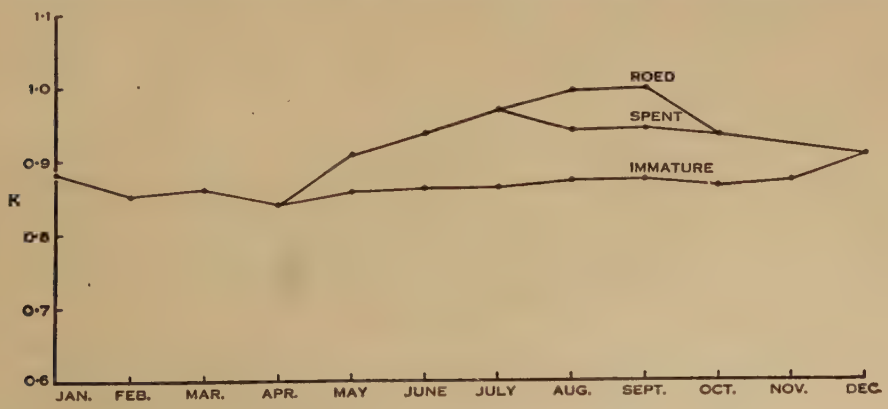

Fig. 3.—Seasonal variation in condition factor, Wilson Inlet.

work the same net has been used in the two areas within a few days and the same difference appears. Yet from scale reading the growth rate and size attained at the

end of each growth period is similar in both areas (Thomson 1957) and the actual size range is the same. This would indicate either that there is such an intensive fishery on the west coast that the majority of fish are taken as soon as they attain the legal

TABLE 1

MODAL SIZE GROUP OF YELLOW-EYE MULLET IN THE WESTERN AUSTRALIAN COMMERCIAL CATCH (CM L.C.F.)

Place	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Peel Inlet	20	20	20	20	21	21	21	21	21	21	21	21
Leschenault Inlet	20	22	22		23		20	21		21		22
Wilson Inlet		23	23	24	25	25			25	24	25	27
Hardy Inlet		20	22	25	23	24	24		23		21	
Nannerup	25	27				25			25	25	24	

minimum length; or that as they grow bigger the fish move into waters where they are not procurable.

TABLE 2

SIZE DISTRIBUTION OF YELLOW-EYE MULLET IN THE COMMERCIAL CATCH, ALL WESTERN AUSTRALIAN WATERS, 1940–1948

L.C.F. (cm)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
18	8	12		2	11	2		3	20			1	59
19	30	26	12	33	38	38	5	8	58	1	1	16	266
20	60	89	59	231	639	185	126	65	71	23	24	49	1621
21	65	193	46	130	773	133	199	47	99	41	25	75	1826
22	13	193	75	82	567	98	113	28	76	17	23	24	1309
23	2	122	254	71	463	76	80	27	94	27	8	19	1243
24	2	46	227	91	269	119	43	7	100	42	2	2	950
25		19	124	89	241	133	17	4	90	17	1	2	737
26		8	157	68	167	71	4	6	105	11		1	598
27		6	118	38	103	53	2	12	49	1			382
28	1	6	44	27	76	30	1	15	23	1			224
29		5	36	22	43	16	2	12	6				142
30			19	12	17	7	2	7	9				73
31			10		6	2		5	7				30
32			9	2	4	1		2	1				19
33			2	4	5			1	1				13
34				1	1								2
35									1				1
Total	181	725	1192	903	3423	964	594	249	810	181	84	189	9495

Although the modal size group is relatively small, in many cases the size distribution of the commercial catch is considerable (Table 2).

The figure suggests that only 3·3 per cent. of the yellow-eye mullet marketed are smaller than the legal size limit of 20 cm L.C.F. (9 in. T.L.).

Some tests were carried out with set nets of different mesh size to determine the range of size and the proportions of each length likely to be caught (Table 3).

TABLE 3

LENGTH FREQUENCIES OF FISH CAUGHT IN MESH NETS OF VARIOUS SIZES

L.C.F. (cm)	Mesh (in.)					
	1¼	1½	2	2¼	2½	3¼
13		1				
14	5			1		
15	93	2		1		
16	218	8	2			
17	65	39	1	2	1	
18	5	65	3	1	1	
19	1	4	5	3	2	
20		2	2	18	4	
21			55	92	8	
22			19	184	6	2
23			10	90	6	2
24			7	31	18	3
25			3	9	4	9
26			2	5	1	14
27				4		7
28						6
29						5
30				2		1
31			1	1	1	
32				1		
Total:	287	121	110	445	52	47
No. of tests:	8	8	8	8	2	2

As far as yellow-eye mullet is concerned, even 2 in. mesh would allow the majority of the catch to be over the minimum legal length. Some few small fish will always be taken. As there is a mixed-species fishery in the estuaries the mesh required will probably depend upon other species of greater girth, particularly the sea mullet.

V. MATURITY

The stages of maturity used in this study are similar to those adopted by Kesteven (1942) for the sea mullet, *Mugil cephalus*, except that his stages III and IV are merged, as in practice it was found impossible to distinguish these in the field. Consequently the stage IV mentioned here is equivalent to Kesteven's stage V and so on.

TABLE 4

SEASON OF GONAD MATURATION, FISH OVER 22 CM L.C.F., WESTERN AUSTRALIA

Gonad Stage: I			II		III		IV		V		VI		VII		Total
Month	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	
January	17	1	2	10		5									35
February	57		7	44		23									131
March												1			1
April	27	11	13	45	1	21		14		3		3			138
May	24	12	34	9	12	22	3	10	10	25	14	24	6	11	216
June											57	53	28	28	166
July											20	15	25	25	85
August									17	16	23	28	32	41	157
September	12	22	11	14	13	22	6	8		3	30	63	14	30	248
October	17	16	17	21	14	23	7	6		1	2	3	1	1	129
November	3	3	2	8										2	18
December	8	8	4	9											29
Total	165	73	90	160	40	116	16	38	27	48	146	190	106	138	1353

The first signs of ripening gonads are found in fish of 18 cm L.C.F., but spent gonads have not been detected in males less than 22 cm or females less than 24·5 cm L.C.F. The examination of gonads of 1353 yellow-eye mullet of more than 22 cm L.C.F. from Western Australia indicated a breeding season over the winter months (May to October) (Table 4).

Maturation appears to be simultaneous along the coast, samples from Wilson Inlet, Leschenault Inlet, Peel Inlet, and the Swan River being at the same stages during the winter months. Insufficient information is available from eastern Australia to make a similar table, but 48 fish taken at Lakes Entrance in Victoria were in stages I to III in December; a sample from Warrnambool Harbour, Vic., in

TABLE 5

EGG COUNTS OF YELLOW-EYE MULLET

Size of Fish (cm)	Estimated No. of Eggs
24·5	125,000
26·6	170,000
28·1	250,000
29·3	440,000
33·7	525,000
35·3	600,000
36·2	625,000
39·1	630,000

January was running ripe; samples from Swansea, Tas., taken in February showed gonads in stage V; and of 39 fish taken in Norfolk Bay, Tas., in March, 9 were spent and the rest in advanced stages of maturity. Fishes of similar size in winter-time had unripe gonads. Hutton (1872) and Graham (1953) state that *A. forsteri* spawns in summer in New Zealand waters.

VI. FECUNDITY

The egg count was estimated gravimetrically. A sample of eight specimens of various sizes showed that the numbers of eggs per female increased with size of the fish (Table 5).

The number of eggs evidently increases severalfold as the female grows larger.

VII. SEX RATIO

The data of Table 4 suggest a sex ratio of 763 females to 590 males: approximately 1·2 females to every male. If samples of less than 10 fish are ignored the ratio becomes 758 females to 460 males or 1·7 females to every male. In the 42 samples making up the latter groups females predominated in all but three. In one of these three samples the numbers of each sex were equal, but in the other two, which were the only sexed samples from catches on sea beaches, males were in excess of females.

TABLE 6

FOOD OF YELLOW-EYE MULLET

Place	Date	No. in Sample	No. Empty	Algal Filaments	Diatoms	Plant Debris	*Corophium*	Other Amphipods	Copepods	*Palaemonetes*	Cladocera	Ostracods	Pelecypods	Gastropods	Polychaets	Chironomids	Sand
Albany	16.xi.1954	23	13	2		1						2	1	6		1	
Leschenault Inlet	23.xi.1954	22	6	10				3	2		1					6	
Wilson Inlet	9.xii.1954	17	11		2	1			3							1	
Leschenault Inlet	19.xii.1954	21	10	9	1							1	2	2			
Leschenault Inlet	10.i.1955	20	12	7	1	2	6					1	4	1	1	3	6
Albany	18.i.1955	21	20							1							
Albany	15.ii.1955	15	14													1	
Leschenault Inlet	20.ii.1955	12	0	2										12			1
Wilson Inlet	14.iii.1955	15	8											7			4
Leschenault Inlet	22.iii.1955	20	6	8	2	1	5	1	2				9	5		3	9
Wilson Inlet	13.iv.1955	16	4		2				2	5				3			
Leschenault Inlet	17.iv.1955	20	18				1		1								
Wilson Inlet	17.v.1955	14	0	1										14	1		
Leschenault Inlet	19.v.1955	21	0	21		2		1	2							10	
Wilson Inlet	10.vi.1955	20	11											8	1	1	
Leschenault Inlet	21.vi.1955	21	6	14	7		2	3	6			1	1			2	1
Brookes Inlet	13.vii.1955	20	5			3	1	2						1		14	12
Leschenault Inlet	19.vii.1955	32	3	8	13	4	1	1	10		2		2			10	23
Albany	9.viii.1955	17	3	7	11	1	1	8	2			3		6			
Leschenault Inlet	16.viii.1955	21	3	10	3	2	9	2	5		2	8		3	3	4	2
Wilson Inlet	6.ix.1955	15	2			1			10	10	1		1		4	1	
Leschenault Inlet	8.ix.1955	25	11	6	2	2	7	1	3			1			1	2	2
Wilson Inlet	11.x.1955	20	6	1	1					10			1	3			
Leschenault Inlet	18.x.1955	22	9	8	1	4		2	6							3	3
Leschenault Inlet	16.xi.1955	18	1	11	11			1	1			1	4	4	2	7	5
Total:		488	182	127	57	24	33	22	45	26	6	21	25	75	13	69	70

TABLE 6 (*Continued*)

Place	Date	No. in Sample	No. Empty	Algal Filaments	Diatoms	Plant Debris	*Corophium*	Other Amphipods	Copepods	*Palaemonetes*	Cladocera	Ostracods	Pelecypods	Gastropods	Polychaets	Chironomids	Sand
No. in which abundant:																	
(*a*) All areas				50	14	0	25	1	8	23	0	2	5	47	3	43	15
(*b*) Wilson Inlet							1		4	21				38	2	2	3
(*c*) Leschenault Inlet				47	10		15		1			2	5	5	1	35	11

Also occurring:

Thrice: fish eggs (garfish?)
Twice: post-larval fish; Foraminifera; sponge; caprellids; isopods; Cumacea
Once: tintinnids; insect larvae (simulid?)

It may be that there tends to be some sexual segregation during the sea run of this species, but the samples are too few to warrant such a conclusion with certainty.

VIII. Food

Thomson (1954*b*) reported on the stomach contents of 127 yellow-eye mullet sampled on six occasions and from various localities. A further 25 samples, totalling 488 stomachs, from Western Australia have since been studied. The study confirmed the earlier finding that *A. forsteri* makes far greater use of animal food than does its relative the sea mullet, *M. cephalus*, in which occasional ingestion of small animals seems to be entirely accidental during the ingestion of algal material. In the yellow-eye mullet many stomachs were found containing animal material only. There were others in which plant material only was present. It appears that yellow-eye mullet will ingest small organic material, whether plant or animal, wherever they come across it (Table 6).

The data cannot be used to determine whether there are seasonal preferences, as there was no concurrent study of the substrate ecology in the various estuaries. It is quite possible that apparent seasonal changes in diet are forced on fish by the presence or absence of food organisms rather than any seasonal change in preference. It is a matter for conjecture whether the individual differences in food found in various yellow-eye mullet taken in the same haul have been caused by fortuitous finding of concentrations of food organisms of different kinds or by the individual's actively seeking the kind of food it prefers.

In most samples there were some empty stomachs. In those recorded in the table as empty, the hindgut also was without contents except sometimes an unrecognizable mush. In one or two instances the majority of the sample had empty guts. However, this could not have reflected lack of food, as in the fish concerned there were extensive fatty deposits along the mesenteries, indicating that feeding had been satisfactory until at least soon before capture. It is possible that individuals do not feel the need for food as soon as the gut is empty but wait a certain period before seeking food.

The type of organisms found in the stomachs indicate that the fish browse on the epiphytes and epizooics of larger algae and of rocks, and perhaps less often on the small benthic organisms of sand and mud banks. *Corophium*, which figured in many stomachs, is a tubiculous amphipod whose tubes are constructed either on algae or rocks, and small tube-building polychaets are also taken. The great majority of copepods found in the stomachs were harpacticoids, which are mostly inhabitants of weed beds. It was apparent from the sand grains included that most of the gastropods and small pelecypods came from sandbanks, but some of these also settle on algae and could be obtained from this source.

Comparing the contents of the stomachs from Leschenault Inlet and Wilson Inlet, which are the only ones well represented in the collection, it is apparent that algal filaments and diatoms play a large role in the nutrition of yellow-eye mullet in Leschenault Inlet, but practically none in Wilson Inlet. In Wilson Inlet gastropods and *Palaemonetes australis* Dakin, a brackish-water shrimp, play a large part in the diet, but the former is only occasionally found in numbers in the stomachs of fish from

Leschenault Inlet, and the latter never. The tube-building amphipods are common in Leschenault Inlet samples, as are chironomid larvae. This presumably reflects the occurrence of organisms in these two bodies of water and not anything peculiar in the nutritional tastes of the fish.

IX. Movements of Yellow-Eye Mullet

(*a*) *General*

During tagging operations for the sea mullet in Western Australia (Thomson 1951), yellow-eye mullet were tagged whenever they appeared in the catches. 1550 were tagged but only 17 (1·1 per cent.) were recovered. No returns were obtained from the majority of tagging operations, the returns from individual tagging operations varying from 0 to 5 per cent. This contrasts with returns from 0 to 25 per cent. from a total return of 2·4 per cent. from the 10,021 sea mullet (Thomson 1955*a*). No facilities were available to hold yellow-eye mullet to test the average length of attachment under controlled conditions or the mortality rate of normal and tagged fish under similar conditions. It may be that the tags were easily torn from the operculum or worked out, or there may have been a differential mortality of tagged fish. One tagged fish was retaken after 936 days, which indicated that the tags could stay on for a considerable period. Some inferences on movements are permissible from interpretation of the seasonal catch distribution.

(*b*) *Outside the Estuaries*

That there are some yellow-eye mullet at sea all the time is obvious from the commercial catches, some being taken, for instance, in all months of the year along the beaches north and south of Fremantle. Whether individuals or schools can maintain themselves at sea permanently is unknown. Only one of the 17 recovered tags came from a fish retaken in waters other than those in which it was tagged. This was a fish tagged at Wonnerup when the estuary was closed and retaken at the breakwater, Bunbury Harbour, 116 days later after the Wonnerup bar had opened.

(*c*) *Inside Estuaries*

Time of freedom before recapture of tagged fish inside the estuaries varied from 1 day to 936 days. The returns were too few to display any pattern of movement. There were five instances in which fish were recaptured within 3 days of being tagged, and each fish had moved well down the estuary when retaken, which suggests that a disturbance or shock may tend to make them seek the sea.

X. Raciation

The species of the family Mugilidae form a most uniform group anatomically, and *A. forsteri* is no exception. Comparison of specimens from the western and eastern coasts of Australia reveals no considerable anatomical variation.

Physiologically the two stocks show a marked difference. Western Australian fish have a winter-breeding period, extending roughly from May to September, whereas eastern fish have a summer-breeding period, December to March. The latter corresponds to the breeding period in New Zealand (Graham 1953). As only immature

fish have been sampled in South Australia, it is not known whether yellow-eye mullet in that State have the breeding characteristics of eastern or western fish.

Morphologically the only difference that has been detected is the distinctly greater number, and correspondingly somewhat smaller size, of the scales in eastern fish. As a result of the difference in spawning time, the size attained at the time of formation of the scale "breaks" differs in the two races (Thomson 1957).

The number of scales in South Australian fish is that typical of Western Australia, perhaps an indication that the population in these waters has the characteristics of western rather than eastern fish (Table 7).

TABLE 7

SCALE NUMBER DISTRIBUTION (ROW VIII)

No. of Scales	Western Australia	South Australia	Eastern Australia
54	22		
55	80	8	
56	51	20	
57	47	15	
58	18	6	
59		1	3
60			21
61			43
62			53
63			11
64			2

XI. IMPLICATIONS FOR THE COMMERCIAL FISHERY

The yellow-eye mullet spawns towards the end of its third year (Fig. 4) at a size greater than the minimum legal length. In Western Australia the individual fish reaches the legal minimum size (20 cm L.C.F. or 9 in. T.L.) at anything from 3 to 10 months prior to spawning, the average being 5 months for males and 8 for females. In Victoria the legal minimum size is 9½ in. T.L. (21·3 cm L.C.F.) and the fish attains this size 2½–5½ months before spawning.

The rate of growth between the time of attaining the minimum legal length and the spawning time is at its most rapid, so that at first glance it might seem advisable to allow the fish to gain this extra weight. However, it is impossible to harvest the entire crop in a short space of time, both because the fishing method is not completely efficient and also because some fish will be in unfishable waters.

It can be seen (Table 2) that relatively few fish are caught after the size attained at first spawning. This might be because of the removal of fish by fishing, but there would be a bias against catching the large fish because of the 2¼ in. and 2½ in. mesh used in the nets (Table 3). Spawning time is also a time of increased mortality rate owing to the concentrated nature of the schools and the debilitation of the fish consequent on spawning. Protecting the fish until they had spawned would succeed only if the gain in weight by the stock exceeded the loss due to mortality. But the experience gained in raising the legal length in Victoria does not suggest that this

experiment would succeed (Thomson, unpublished data). Thomson (1955*b*) has already expressed the opinion that the best legal minimum size is that attained about half way during the growth season prior to reaching maturity, as a compromise between the desire to harvest the greatest weight and the inability of the fishing

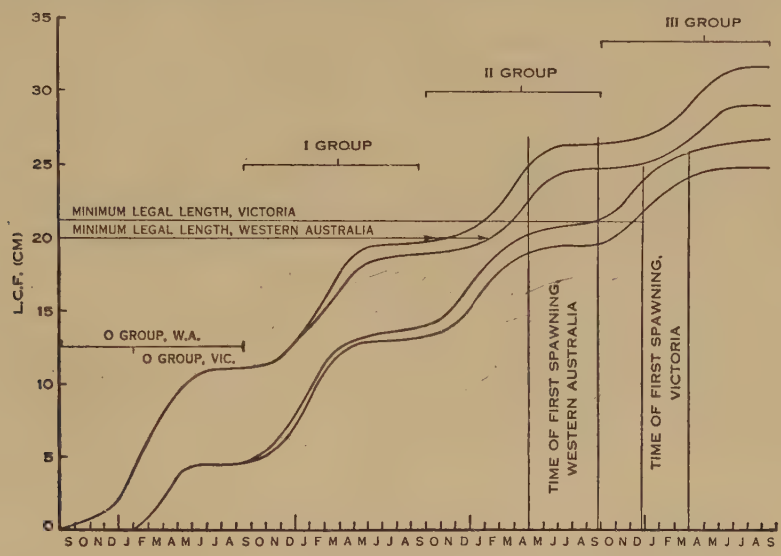

Fig. 4.—Seasonal growth curve for four years, demonstrating the time of onset of maturity and the legal minimum length.

method to achieve this in a short period of fishing. In the absence of any evidence that insufficient fish escape to provide an adequate spawning stock, or that the fecundity of the fish is dangerously low (Section VI), it would seem that the present legal minima are quite adequate.

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INTERPRETATION OF THE SCALES OF THE YELLOW-EYE MULLET, *ALDRICHETTA FORSTERI* (CUVIER & VALENCIENNES) (MUGILIDAE)

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Summary

The yellow-eye mullet scale is of the typical percomorph type, feebly ctenoid in most cases, but cycloid in the mid-flank region, which provides the best scale for age and growth determinations. The annual "break" is more obvious in the posterior sector than in the anterior. Above a length of 5 cm (length to caudal fork) there is a straight-line relationship between increments in dimensions of scale and increments in length of the fish. The scales of Victorian and Tasmanian fish are smaller than those of Western Australian fish, which is in accord with the rather larger number of scales in eastern fish. The annual "breaks" become apparent in spring when growth recommences after the winter cessation. As western fish are winter spawners and eastern fish summer spawners, the age and size attained at the time of formation of the annuli differs in the two stocks. Females grow faster than males. Lengths (cm) attained each winter average as follows:

Year	I	II	III	IV	V	VI	VII
Western fish	11	18–19	24–25	29–32	32–35	38	39
Eastern fish	5	12–13	19–21	24–27	30		

The Petersen method of modal progression gives rather higher readings in the first and second years, probably as a result of mesh selection.

I. Introduction

The scales of fish have been used frequently to estimate the age and rate of growth of fish. As Van Oosten (1941) has emphasized, it should not be assumed that scale growth bears a constant relationship to the increase in body length, or that each break or zone of slow growth necessarily indicates a year's growth since the previous break or zone was formed. In order to facilitate the study of the growth rate of the yellow-eye mullet, *Aldrichetta forsteri* (Cuvier & Valenciennes), a critical analysis of the scale pattern and structure is presented here. Most of the data are available from Western Australia. The majority of the fish referred to as "eastern" in this paper come from Victoria and Tasmania, though some unsexed and mostly immature material from South Australia and southern New South Wales was also studied.

II. Scale Pattern

On each side of the body of *A. forsteri* 16–18 rows of imbricated scales can be counted diagonally between the first dorsal and the ventral fins. In the ensuing discussion the most common number of rows, 17 (165 of 184 fish inspected), will be assumed. These rows, running from the pectoral fin region to the base of the caudal fin, grow fewer towards the tail, there being only 12 at the least depth of the caudal

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peduncle. As a datum point from which any scale may be particularized, the second scale above the anterior end of the pectoral fin base is taken (the first scale above the base is minute and distorted). This is the first scale of the eighth row of scales, counting downwards from the first dorsal fin. It will be referred to as scale VIII, 1, in the notation adopted. Counting diagonally cephalad upwards (not far from the vertical in this part of the body) scales 1 of rows VII to III are clearly distinguished. But above III, 1, the distorted unevenly spaced head and back scales are found. Row II does not commence as a distinguishable row until the level of the eighth scale of the rows beneath it. Its first scale is therefore referred to as II, 8. Similarly row I does not commence until scale I, 18, about four scales in front of the first dorsal fin origin. Ventrally from row VIII the pectoral fin occupies the area where the first few scales of the rows immediately ventral to row VIII would lie. Rows IX to XI commence at scale 3, counting diagonally caudad from VIII, 3. At the lower corner of the pectoral there is a patch of small distorted scales, and it is impossible to distinguish any continuation of the more ventral rows amongst these. Hence rows XII to XVII commence at scale 5. It is possible to follow rows XIV to XVII forwards, but the scales in the triangle anterior to the line connecting scales XI, 4, and XVII, 5, are distorted and cannot be utilized in age and growth studies.

Posteriorly the scale rows become reduced as the body depth lessens. Row I, after being disrupted by the obbasal scale of the first dorsal fin and its preceding small misshapen scales, continues to the origin of the second dorsal. Rows II and III merge five or six scales in front of the base of the caudal fin. Rows XIV and XV merge about half way along the anal fin. Row XVI ends at the anal fin origin and row XVII at the anus.

The datum row, VIII, has 54–58 scales in Western Australian fish, 55–59 in South Australian fish, and 59–64 in those from the more eastern waters. Typical scale numbers per row for western fish are shown in Table 1. There are minute scales on all the fins except the first dorsal and four or five of intermediate size between the body scales proper and the minute scalation of the caudal fin. These and the three rows of cheek scales are useless for age or growth studies.

III. Scale Form

(a) *Surface Appearance*

The scales of the dorsolateral region are almost symmetrical. Away from this area they become distorted in varying degrees. Scale VIII, 16, which lies under the tip of the pectoral fin, may be taken as typical (Plate 1). It has almost straight anterior (basal) and lateral borders. The posterior (apical) border is rounded. Thomson (1954) described the scales of this species as cycloid except on the cheek, but actually many of the body scales are feebly ctenoid. In fact only some of those scales on the flat portions of the flanks (scales 7–37) are cycloid. Table 1 shows that rows IX–XI have more cycloid scales than the others. The scales of dorsal rows I–VI and the ventral rows XIII–XVII are all ctenoid, those of rows I–III and XIV–XVII strongly so throughout.

The nucleus (the focus of Taylor (1916) and Lagler (1947, 1950)) is displaced posteriorly owing to unequal growth of posterior and anterior fields (Plate 1). From

the small blank area of the nucleus diverge an anterior and a posterior pair of axes, termed the shoulders, which divide the surface area into four sectors—the anterior (basal), posterior (apical), and two lateral fields. These fields are delineated by changes in direction of the circuli (see below) and sometimes by changes in the number of circuli, and also by more or less prominent ridging of the shoulders, of which the anterior pair are prominent, giving the illusion that the anterior sector lies in a plane differing from lateral fields. The posterior shoulders are discernible under the microscope or when the image is projected, but they are not obvious to the naked eye.

TABLE 1

RESUMÉ OF SCALE PATTERN OF 18 WESTERN AUSTRALIAN MULLET OVER 21 CM L.C.F.*

Row	Determinable Scales	No. of Asymmetrical Scales	No. of Cycloid Scales	No. with Mucous Canal	Anteriormost Scale with Length Greater than Breadth
I	18–28	8	0	4	22
II	8–44	19	0	34	24
III	1–59	17	0	35	26
IV	1–56	8	0	36	26
V	1–51	2	0	29	26
VI	1–52	6	0	24	26
VII	1–53	8	7	31	26
VIII	1–54	12	7	40	26
IX	1–53	12	19	30	25
X	3–53	6	20	33	22
XI	3–55	18	14	40	20
XII	5–54	15	10	45	17
XIII	5–52	23	0	48	15
XIV	5–52	25	0	41	14
XV	5–36	20	0	32	12
XVI	5–34	20	0	32	12
XVII	5–26	21	0	22	8

* Length to caudal fork.

The shoulders are referred to as radii by Pillay (1951), but this term usually refers (Cockerell 1913; Taylor 1916; Lagler 1950) to the grooves diverging from the nucleus towards the edge of the anterior sector. Primary radii diverge from the nucleus. Secondary radii may develop further out as the scale increases in area. A typical scale from the mid-lateral region has 4 primary radii and there may be 4–10 secondary radii.

Outside the nucleus the scale is marked by lines known as circuli (or striae) which are more or less parallel within each field. The number of circuli in the anterior field is approximately double the number in the lateral fields, where a circulus may meet anything from one to four circuli of the anterior field. The posterior field has as many circuli as the lateral fields except that several extra ones occur in the

vicinity of the "annuli", which will be described below. There are no initial circuli differing from the true circuli in the vicinity of the nucleus as described for *Mugil cephalus* Linnaeus by Jacot (1920) and Pillay (1951).

The regular disposition of the circuli is broken by lines or "breaks" which may tentatively be identified as annuli, since they have all the characteristics listed by Kesteven (1942) for the annuli of *Mugil cephalus* (syn. *M. dobula* Günther) except that they differ in being most prominent in the posterior field instead of the anterior. (It should be noted that Kesteven (1942) has the notation of anterior and posterior reversed from that adopted here and by most authors, and from the natural position of the scales on the fish.)

(*b*) *Mucous Canals*

Mucous canals are frequent on mugilid scales. Fée (1869), Jacot (1920), and Pillay (1951) referred to them as being part of the lateral line canal system. Mugilids have no prominent lateral line such as is found in many fish. But the mucous canals are found in at least some of the scales in every row (Table 1) and no canal system joins them in any way. The underlying cells seem to be not neuromasts but of a secretory nature. Scales with mucous canals are most frequent in rows XI–XIV. Only row I has fewer scales with mucous canals than without. The mucous canal generally runs through or close to the nucleus but occasionally it may be displaced considerably from the nucleus (Plate 2, Fig. 1), probably as the result of displacement of the scale. The mucous canal is hollowed out of the outer surface of the scale and consists of two portions, a posterior basal portion which is wider and deeper, usually ending at the level of the nucleus, where it is continued in the narrow shallow anterior canal. Connexion to the under-side of the scale is through a minute tissue-plugged pore in the trough of the basal portion of the mucous canal. The anterior canal is sometimes in a straight line with the posterior but more usually it is at an angle to it. The base itself may lie at any angle between about 40° on either side of the long axis of the body, and the anterior canal may turn up or down from it. The canals generally turn up and down alternately in a row of scales, though sometimes successively two, but rarely more, may turn the same way. The mucous canal of this species covers only about a fifth of the length of the scale. Occasionally the basal portion is duplicated, probably as a result of partial rotation of the scale in its socket, such as Van Oosten (1929) has described, for such scales usually show a double nucleus. Even more rarely, and usually on distorted scales near the tail, the anterior canal may be duplicated.

(*c*) *Granulated Scales*

Two types of granulated scales were found on *A. forsteri*. In one type the granulations were irregular in outline and mostly confined to the anterior and posterior fields (Plate 2, Fig. 2). Van Oosten (1929) has suggested that such granulation is due to repair of local injuries to the edge of the scale at a younger stage. The present granulations suggest rather a corrosion of the scale. The second type of granulation is that found on scales commonly referred to as eroded or regenerated, or more correctly as replacement scales. In such scales the granulated area is more

or less even in outline (Plate 2, Fig. 3). Outside the central granulated area, which represents the amount of growth the regenerated scale had to make to reach approximately normal size, the scale has the attributes of a normal scale, except that radii tend to be more numerous in replacement scales, and mucous canals and ctenii are redeveloped only on those which are replaced at an early stage (usually before the formation of the first annulus). Replacement scales also tend to be of slightly smaller dimensions than the original scale would have been.

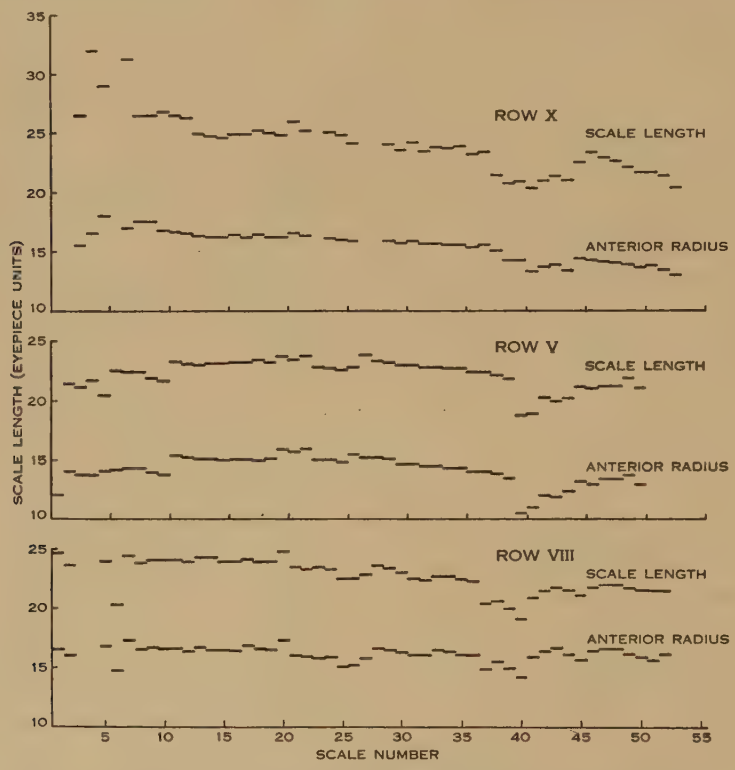

Fig. 1.—Comparative scale lengths and anterior radius lengths (arbitrary micrometer eyepiece units) of scale rows V, VIII, and X, of a fish 25·8 cm L.C.F. from Wilson Inlet, W.A.

(*d*) *Size and Dimensions of the Scales*

The proportions of the scales vary. The nucleus is nearer the posterior edge of the scales farther posterior along each row. Considering those scales which are symmetrical or only slightly asymmetrical, the more anterior are wider than long; whereas those behind scale 25 or 26 of the mid-flank region, and even farther forward in other rows, have the scale longer than broad (Table 1).

The size of any particular scale dimension is not uniform over the fish's body. So although there may be a constant relationship between the size of the fish and any particular scale (Section IV (*a*) (ii)), the mathematical relationship will vary with each

scale. Consequently, in sampling, either a particular scale would have to be used from each fish, which would entail greater time in locating the key scale which might be missing or granulated, or a group of scales whose dimensions differ only slightly could be utilized. Figure 1 shows the whole scale length and anterior radius length from three selected rows (V, VIII, and X). It is apparent that the scales are most uniform in this dimension between scales 12 and 22, that is, roughly in the region reached by the tip of the pectoral fin.

IV. Age and Growth Studies

(*a*) *Appraisal of the Scales*

As stated above, there are marks or breaks on the scales which seem to correspond to the annuli of *M. cephalus* described by Kesteven (1942). Van Oosten (1929) and Lagler (1950) have listed the conditions under which these "annuli" may be considered as year marks.

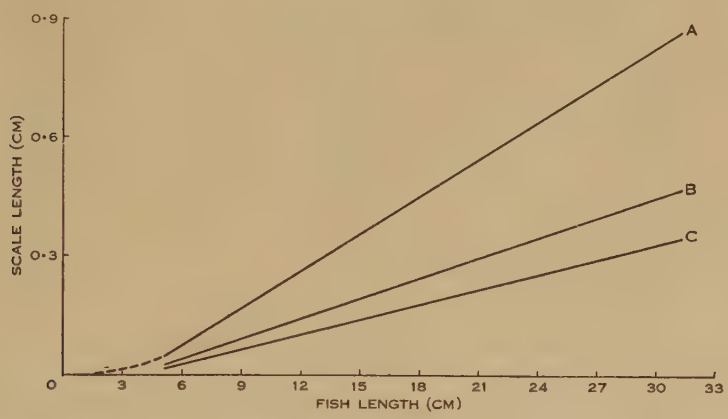

Fig. 2.—Correlation of fish length with: *A*, length of scale; *B*, length of anterior radius; *C*, length of posterior radius.

(i) *Constancy in Number and Identity of Scales.*—The nuclear area of scales from older fish is identical in appearance with the scales of young fish. Regenerated scales have a typical granular central part. The number of scales appears to be constant in an individual. It has not, of course, been possible to check this on an individual fish, but although the lateral count of scales varies from 54 to 58 there is no correlation between number of scales and size of fish.

(ii) *Correlation between Growth of Body and Scale.*—Scales from rows VI–X in the vicinity of the tip of the pectoral fin are relatively uniform in size (Fig. 1). Figure 2, illustrating the relationship of scale length to length of fish, was prepared using scales from this region. There is considerable scatter about the line of best fit which, however, appears to be a straight line. Calculated from data on 1789 fish from Western Australia and 297 from eastern Australia between the sizes of 5 and 31·5 cm, the regression line formulae of whole scale length (*SW*) (anterior-posterior axis), of anterior

radius (S_a), and of posterior radius (S_p) on length to the caudal fork (L) for Western Australian and eastern Australian fish are as follows:

Western Australia	Eastern Australia
$L = 3{\cdot}57 + 33{\cdot}4S_w \pm 2{\cdot}76$	$L = 3{\cdot}58 + 34{\cdot}7S_w \pm 2{\cdot}01$
$L = 3{\cdot}46 + 59{\cdot}8S_a \pm 2{\cdot}91$	$L = 3{\cdot}16 + 60{\cdot}3S_a \pm 3{\cdot}25$
$L = 3{\cdot}25 + 77{\cdot}6S_p \pm 5{\cdot}22$	$L = 4{\cdot}82 + 72{\cdot}0S_p \pm 5{\cdot}61$

This indicates that in correlation with the somewhat larger number of scales on eastern Australian yellow-eye mullet (Section II) these fish have scales which are slightly smaller than those on Western Australian fish of the same size; the anterior radius of eastern scales is proportionately large and the posterior small compared with western scales.

TABLE 2

SEASONAL GROWTH OF II+ YELLOW-EYE MULLET CALCULATED FROM MARGINAL INCREMENTS OF 1025 FISH

All localities Western Australia. Measurements in centimetres

No. of Annuli	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1	4·7	7·0	7·4	8·6	8·5	8·5	8·4	8·3	8·8	0·6		
2	4·7	6·4	6·8	5·9	7·0	7·2		7·2	7·2 (1·1)*	1·0	2·0	3·8
3	3·6		4·3	4·8	5·5	5·9			5·7 (0·5)*	0·8		
4		2·7	3·1		4·1	4·2		4·1	4·1			
5			2·0									
No. of fish:	116	84	210	188	386	177	78	101	200	115	20	84

* The figures in parenthesis indicate the increments at a later date in the month.

Such relationships rarely, if ever, hold at small sizes (see Lagler 1950 for brief review). These formulae would indicate that the scales appear at a fish length of 3·0–4·8 cm. Field collections of young fry indicate that scales appear at about 1·8 cm. This implies a curve towards zero at the lower end of the regression line as figured by Ricker and Lagler (1942) for the white crappie *Pomoxis annularis* Rafinesque and the large-mouth bass *Micropterus salmoides* (Lacépède), whereas Blackburn (1949) and Miller (1955), studying clupeoids, found a curve away from zero; in other words, in the clupeoid studies, the size at first appearance of the scales was greater than that indicated by the regression line.

(iii) *Frequency and Time of Formation of the "Annuli"*.—The marks and breaks referred to in Section II as annuli appear at intervals upon the scales of larger yellow-eye mullet. Examination of scales collected at various times of the year will show when the annuli are formed. The marginal increments, i.e. the width of the scale border outside the annuli, are smallest in late September and early October (Table 2). The size of marginal increment is practically the same from June to September, indicating that growth in all age groups ceases during July, August, and early September. The annulus thus becomes apparent when the scale starts to grow

in the spring, a situation paralleling that found in the sea mullet (*Mugil cephalus* Linnaeus) in the same waters (Thomson 1951).

The possibility that seasonal growth of scale and fish might not be contemporaneous is disproved by graphing the mean values of scale size from fish of a selected length taken at different times of the year. The graph (Fig. 3) shows a normal scatter about an average value and not a sine curve as found by Duff (1929) for cod.

(*b*) *Age for Size*

As all the rings are formed at the same time of the year, those subsequent to the first will appear at yearly intervals and thus give a valid indication of the age since the appearance of the first annulus. The first annulus will form at the end of the first 12 months of life only in those fish spawned in late September (the time when

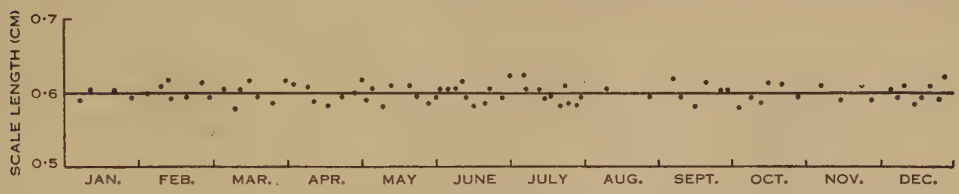

Fig. 3.—The scale size of fish of 20 cm L.C.F. taken at various times of year.

the annulus appears). In Western Australia this is the end of the 4-month spawning season. In the eastern States yellow-eye mullet spawn from December to February (Thomson, unpublished data). Consequently the first scale ring or annulus of a western fish may appear 9–12 months after spawning; but in eastern fish only 7–9 months after spawning. It also means that western fish have a 9- or 10-month growing period before growth ceases in winter, whereas eastern fish have only 4–6 months' growth. Consequently the first annulus on the scales of eastern fish is formed at a much smaller size than on those of western fish.

In the discussion that follows, the usual notation of 0, I, II, etc., for age groups will be used, although this will designate fish with scales bearing corresponding numbers of annuli and will not necessarily imply that the fish are less than 12 months old, 12–24 months old, etc.

Because of the spread of spawning over several months the range of size attained at the time of formation of the annuli is considerable. As a result the age group to which a fish belongs cannot be gauged from its length alone; the time of year at which it is taken has also to be taken into account. Table 3 shows the age-for-length distribution for fish from Western Australia. There are insufficient data on the older age groups from eastern Australia to provide a similar table. Of the 1759 readable scale samples from Western Australia, 1536 had data on sex available; similar data were available for 83 of the 273 scales from eastern fish. It is quite evident that, age for age, female fish are larger than males. The oldest fish taken during sampling (and these were the largest yellow-eye mullet the author has seen at any time) belonged to age group VII. But few females and still fewer males seem to live more than 5 or 6 years.

Table 3 can be interpreted as meaning: (1) In Western Australia, 0 group fish comprise all yellow-eye at 6 cm or less, and some up to 11 cm; (2) the I group include some between 6 cm and 11 cm, all between 11 cm and 13 cm, and some between 13 cm and 19 cm.

TABLE 3

MALE AND FEMALE AGE-FOR-LENGTH DISTRIBUTION, WESTERN AUSTRALIA

Length, L.C.F. (cm)	Male					Female						
	I	II	III	IV	V	I	II	III	IV	V	VI	VII
13	7					2						
14	3	1				2						
15	2	2				2	1					
16	1					1	1					
17	2	8				3	2					
18		14				5	9					
19		26	1			1	27					
20		41	19				53	2				
21		25	30				40	25				
22		5	40				16	70				
23			39	1			6	39				
24			34	6			2	42	3			
25			16	15				40	9			
26			5	20				43	41			
27				27	4			14	39			
28				12	10			2	38	1		
29				3	6				30	4		
30					3				13	16		
31									4	22		
32										15		
33										4	2	
34										4	7	
35												
36											1	
37												
38												1
39												1
Total	15	120	184	84	23	16	157	277	177	66	10	2

The older age groups can be interpreted similarly, with the added complication of the sexual differences, which become clearly established in the third year.

(c) *Growth Rate*

Direct evidence of growth rate can be obtained by measuring fish at time of tagging and at recapture. Such evidence is lacking for yellow-eye mullet, as the operculum tag used in the contemporaneous study of the sea mullet (Thomson 1951) did not prove suitable for long periods of attachment on yellow-eye.

The growth rate has therefore been estimated from scale reading, and some measure of independent check is given by the Petersen technique of interpreting the modes of a graph of size distribution as the modal lengths of successive year groups.

(i) *Annual Growth.*—It has been demonstrated in Section IV(*a*)(ii) that the increments of scale size and body bear a constant relationship to each other. As a consequence of the non-linear relationship of scale and fish lengths before a size of

TABLE 4

INTERMEDIATE LENGTHS, WESTERN AUSTRALIA

Annulus:	I	II	III	IV	V	VI	VII
Male:							
Length (cm)	11·09	18·97	24·71	29·23	32·76		
Number	426	411	291	107	23		
Female:							
Length (cm)	11·20	19·68	26·42	31·74	35·21	37·90	39·33
Number	905	889	532	255	80	12	2

5 cm is reached, the relationship is between the increments and not the absolute sizes, and therefore the size of the fish at any intermediate length cannot be estimated from the dimensions of the scale by simple proportion.

The intermediate length as calculated by simple proportion must be "corrected" by use of the formula

$$L_n = L'_n + A\left(1 - \frac{L'_n}{L}\right),$$

where L_n is the required intermediate length; L'_n is the estimate of the intermediate

TABLE 5

INTERMEDIATE LENGTHS, EASTERN AUSTRALIA

Annulus:	I	II	III	IV	V
Male:					
Length (cm)	5·00	12·87	19·55	24·88	
Number	32	12	4	2	
Female:					
Length (cm)	5·23	13·56	20·99	26·72	30·61
Number	51	28	15	10	3

length obtained by simple proportion; A is the Y-intercept constant in the appropriate regression equation describing the relationship between scale and fish length; and L is the length of the fish when sampled.

The mean lengths to the caudal fork (L.C.F.) attained each year at the time of formation of the annuli are shown in Tables 4 and 5.

The female yellow-eye mullet clearly grows at a greater rate than the male. The difference in the first year's growth is not significant, but in subsequent years the difference is clearly established.

The actual rate of growth of the eastern fish seems to be similar to that of the western fish as the curves are parallel, but owing to the different time of spawning of the eastern stock, the absolute size at the time of formation of the annulus differs.

TABLE 6

LOCAL VARIATION IN MEAN CALCULATED INTERMEDIATE LENGTHS (CM L.C.F.)

Locality	l_1		l_2		l_3		l_4		l_5		l_6	l_7
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♀	♀
Bowes River		11·1		19·7		25·5						
Swan River	8·1	8·8										
Safety Bay	9·4	9·0	19·6	20·0								
Whitford's Beach	9·0	10·2	18·0	21·1	23·6							
Peel Inlet	8·7	9·4	18·4	19·0	24·1	26·4		31·5				
Leschenault Inlet	9·1	9·1	18·7	19·2								
Margaret River	11·4	11·5	18·8	18·9	25·8	27·2						
Hardy Inlet	10·3	10·2	19·1	19·7	25·6	26·9		31·8				
Nornalup	11·2	11·4	19·7	19·9								
Brooks Inlet		11·3		19·8		26·5		32·4		35·6	37·8	
Irwin Inlet	9·9	10·1	18·0	19·9								
Wilson Inlet	10·7	10·8	19·4	20·7	24·1	25·9	28·4	31·8	32·8	35·2	37·9	39·4
Torbay	11·5	11·5	19·3	19·8	25·0	27·1		31·9				
Oyster Harbour	10·2	10·3	18·5	18·4	24·2	26·3						
Nannerup	11·2	11·1	19·6	20·0	25·9	27·1	28·8	32·2		36·2		
Bandy Creek		11·7		20·1		28·2		32·8				
Hopetoun	11·3	11·0		19·1		25·8						

There is some local variation in growth rate (Table 6).

The means from all districts are fairly close despite the wide variation in individual size at the time of formation of the annulus (Section IV(*c*)(iii)). There is more variation apparent at the time of formation of the first annulus than later, the difference between the lowest locality mean and the highest in Western Australia being 25 per cent. of the grand mean for the State. The absolute difference remains much the same over the years but the proportional difference declines with age.

There is no continuing trend of growth at a slow or fast rate in any particular locality. This can be seen from Table 6, but is more clearly expressed in Table 7, where annual differences are recorded for certain localities from which adequate samples are available. Annual variation in growth rate occurs in the various localities as illustrated by Wilson and Peel Inlets (Table 7). As sexual difference in growth rate is very small in the first 2 years (Table 4) this factor is ignored here.

(ii) *Individual Growth.*—The growth data presented in the preceding section were derived from the means of group samples and indicate the general trend of

growth for the stock as a whole. The individual growth curve may vary significantly from that of the hypothetical average fish as shown in Figure 4.

(iii) *Seasonal Growth.*—It has already been shown in Table 2 that growth generally ceases in July, August, and early September, at least in Western Australian waters; it is also apparent from the cumulative increments that growth is most rapid during midsummer—December to February.

TABLE 7

ANNUAL VARIATION IN LENGTH AT TIME OF FORMATION OF FIRST AND SECOND ANNULI, WILSON INLET AND PEEL INLET

Year Class	Wilson Inlet		Peel Inlet	
	l_1 (cm)	l_2 (cm)	l_1 (cm)	l_2 (cm)
1935	10·31	20·55		
1936	11·65	19·07	8·80	18·75
1937	9·24	18·79	9·33	19·01
1938			7·95	17·66
1942	10·53	19·51	8·58	18·54
1943	9·72	19·76	9·07	18·98
1944	10·53	19·09	9·12	18·65
1945	9·96	18·87	8·77	18·21
1951	8·98	18·06		
1952	10·00	19·75		
1953	9·02	19·11		

(*d*) *Confirmation of Scale Analysis by the Petersen Method*

Petersen's method of interpreting the modes of a graph size distribution as the modal lengths of successive year groups can be used successfully when there are short spawning periods and marked annual growth.

Although the spawning period of the yellow-eye mullet is prolonged over several months and the sexes display different rates of growth in later years, the first three size groups can be traced by this means (Fig. 5). From the modes of the curves at the end of winter or in early spring, corresponding to the time of formation of the annuli, the size of the three year groups at this time would appear to be approximately 15, 20, and either 24 or 26 cm respectively. The first figure is markedly higher than that obtained by scale reading (Table 5) but is probably due to the catching bias of the net used ($1\frac{1}{4}$ in. mesh), the fish of this group being taken in experimental hauls. The second year group is marked at 20 cm by the Petersen method and somewhat below this by scale reading. Again this could be due to bias of the nets, as the fishermen aim at catching as little as possible below 20 cm L.C.F. (= 9 in. total length) which is the legal minimum length in Western Australia. The alternative figures for the third year group, derived from the curves for August and September, accord

well with the scale reading results for the two sexes and might be conceived to be the result of a preponderance of a different sex in the two months.

The growth rate as portrayed by the progression of the modes shows a maximum from January to March, which accords well with the figures obtained for the marginal increments of the scales in those months (Table 2).

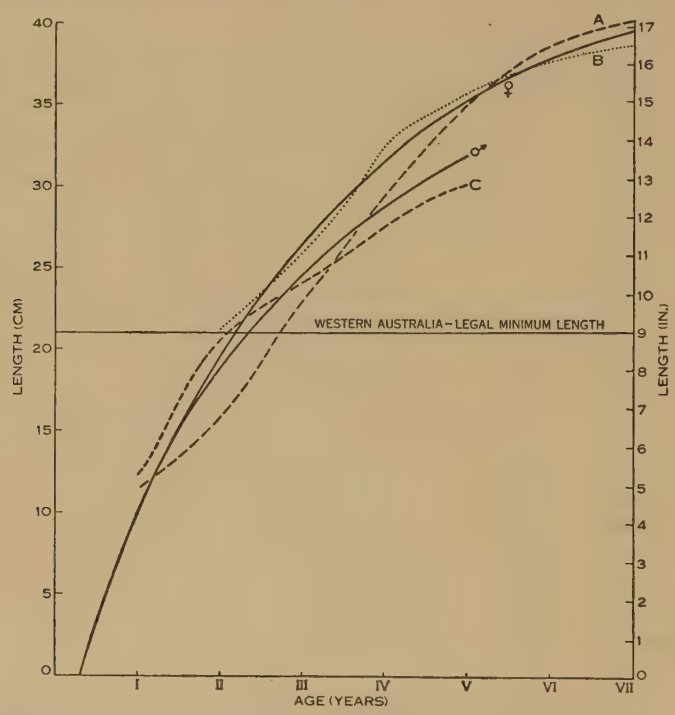

Fig. 4.—Annual growth curve for males and females (solid lines), and individual growth curves for two females (*A* and *B*) and a male (*C*) derived from scale readings.

V. Conclusions

Age and growth studies of the yellow-eye mullet may be successfully carried out by taking scales from the mid-flank region. Scales from other parts of the body are more or less distorted or obscured by ctenii or proliferation of the mucous canal. Scale rows VII–XII include cycloid scales which are easiest to read; the other rows are ctenoid throughout.

Annuli are formed by marks on the scale appearing when growth recommences in spring following a winter cessation. Scale reading suggests that on the average, fish which have formed the first annulus attain a length of 11·1 cm in Western Australia and about 5·16 in the eastern States; second year fish are 18 or 19 cm in the west and 12·5 to 13·5 in the east; third year fish 24–26 and 19–21 cm respectively; fourth year fish 29–31·75 and 24·5–26·75 cm; fifth year fish 32–35 and 30 cm; and in the west a few sixth and seventh year mullet have been taken at 37·9 and 39·3 cm.

The Petersen method gives rather higher readings for the first and second year but these probably result from the catching bias of the nets sampling the population. The differences in size at formation of annuli between eastern and western fish are due to the different spawning seasons—summer in the east, winter in the west.

Females grow rather faster than males, as becomes apparent in the third year. Seasonal growth rate is greatest in midsummer; growth virtually ceases in midwinter.

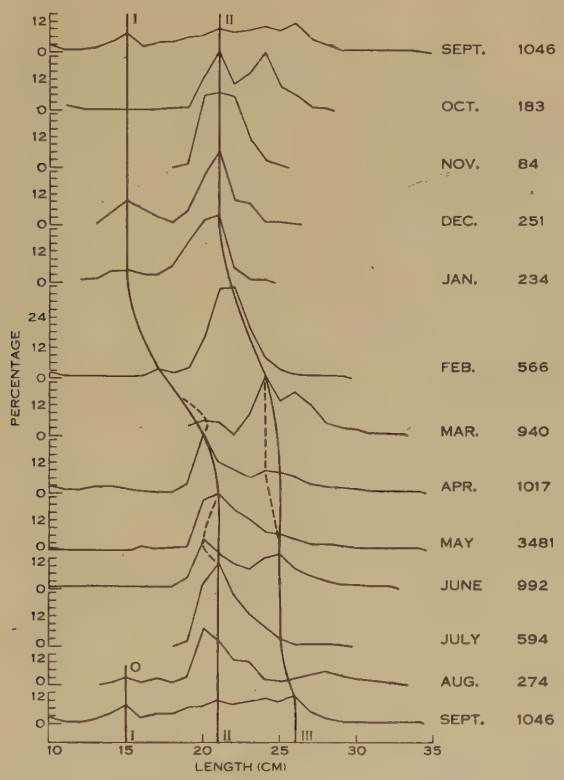

Fig. 5.—Monthly length frequency distribution from Western Australian market samples and experimental hauls, illustrating progression of the modes of year classes I and II.

VI. Acknowledgments

Some of the early material used in this work (1939–1941) was collected at the instigation of Dr. G. L. Kesteven. The author collected most of the remaining material, assisted by Mr. L. Smith of the Department of Fisheries in Western Australia. The figures were prepared by Mr. R. Breach.

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Scale VIII, 16, from a III+ fish, 25·2 cm L.C.F. A typical scale.

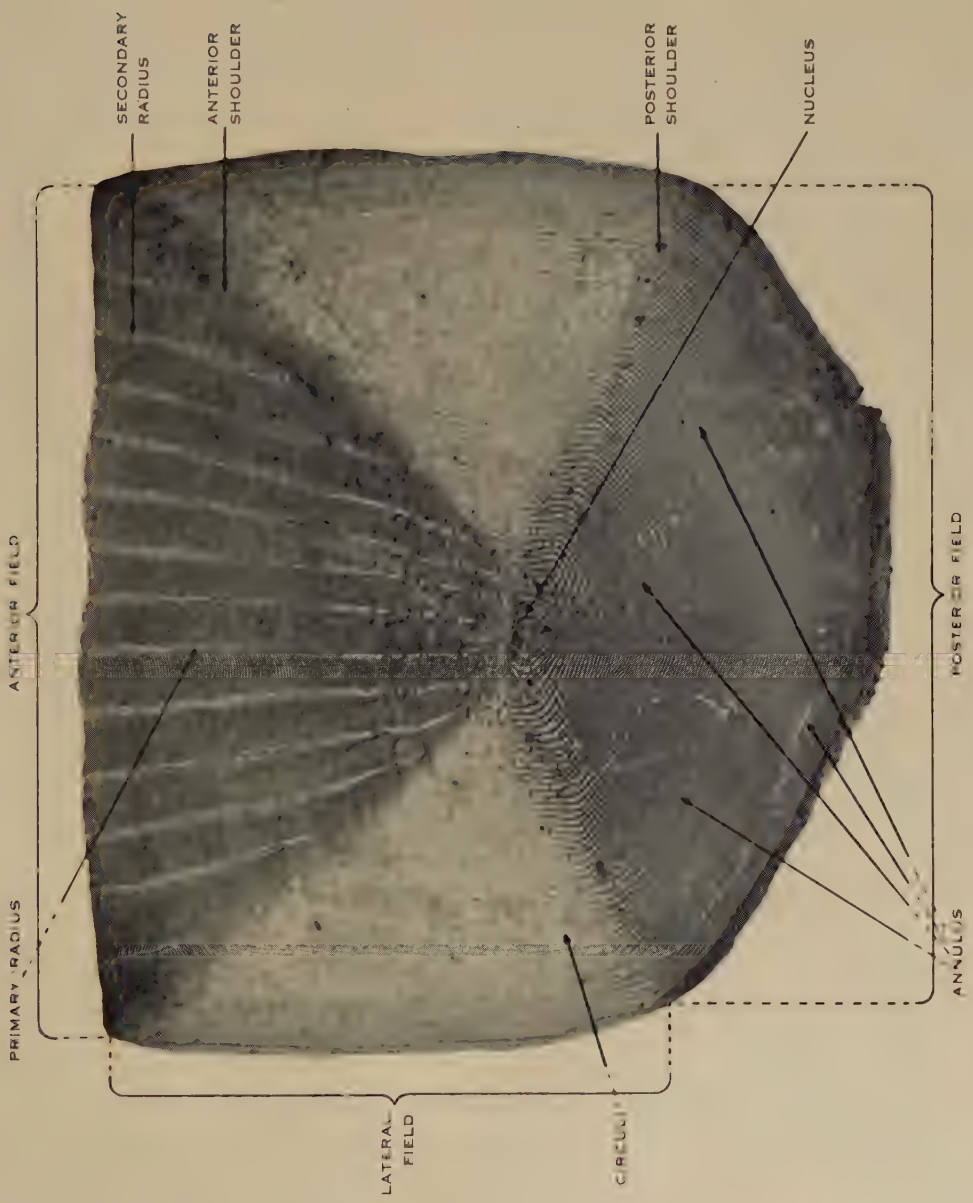
PLATE 2

Fig. 1.—Scale X, 17, from a III + fish, 25·2 cm L.C.F., showing double nucleus and displaced mucous canal.

Fig. 2.—Scale VII, 28, from a IV + fish, 26·2 cm L.C.F., showing irregular granulations.

Fig. 3.—Scale IX, 16, from a III + fish, 23·0 cm L.C.F., replacement type of granulation.

SCALES OF YELLOW-EYE MULLET



SCALES OF YELLOW-EYE MULLET

THE RELATION BETWEEN THE FOOD OF THE AUSTRALIAN BARRACOUTA, *THYRSITES ATUN* (EUPHRASEN), AND RECENT FLUCTUATIONS IN THE FISHERIES

By M. Blackburn*

[*Manuscript received August* 1, 1956]

Summary

The diet of surface-swimming Australian barracouta was studied from over 10,000 stomachs.

The principal prey organisms in Bass Strait are the euphausiid *Nyctiphanes australis* Sars, the anchovy *Engraulis australis* (White), and young barracouta, in that order; and in eastern Tasmania *Nyctiphanes*, *Engraulis*, and the sprat *Clupea bassensis* McCulloch, in that order. The pilchard *Sardinops neopilchardus* (Steindachner) is not an important item of the diet in these regions although it is so in New South Wales, South Australia, and Western Australia. The jack mackerel *Trachurus declivis* Jenyns is a significant item in eastern Tasmania and New South Wales but not in Bass Strait. These and other features of the fish diet of the barracouta reflect actual availability of the various small fish species in the waters. Barracouta eat *Nyctiphanes* by herding them into dense masses (or finding them already concentrated) and swallowing them.

The movements of the anchovy make it unavailable to Bass Strait and eastern Tasmanian barracouta for much of the summer and autumn period, when the barracouta are thus dependent upon *Nyctiphanes* for the bulk of their food. A close positive relationship between the availability of barracouta and *Nyctiphanes* might therefore be expected at those seasons. There is evidence of such a relationship between mean availability (catch per boat-month) of barracouta and mean percentage of barracouta stomachs containing *Nyctiphanes*, at those seasons, from year to year. For southern Victorian coastal waters both show a downward trend from 1948–49 to 1950–51 and then an upward trend to 1953–54; for eastern Tasmania both show a downward trend (for autumn only) from 1949–50 through 1952–53. The records of catch per boat-month furnish independent evidence that the main variations in this index were effects of availability (population distribution or behaviour) rather than abundance (population size), at least for southern Victoria.

It is therefore considered that when scarcity of barracouta occurs in summer and autumn in the coastal fishing areas it may be due to scarcity of *Nyctiphanes*, forcing the fish to go offshore for this food which is known to be available there. This would take the fish out of range of the fishermen.

I. Introduction

The purpose of this paper is to describe the main features of the diet of the barracouta, *Thyrsites atun* (Euphrasen), in Australian waters, especially those of Victoria and Tasmania where most of the commercial catch is taken, and to discuss their bearing on recent fluctuations in the availability of the species to coastal fishermen.

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Many species of animals eaten by barracouta still await identification, and only the few which consistently account for the greater part of the diet are considered here. The total number of stomachs examined was 10,181.

The barracouta which were studied were caught by normal commercial fishing methods, i.e. trolling and pole-fishing at the surface of the sea. They ranged from 40 to 116 cm in length, measured from the most anterior part of the head to the caudal

Fig. 1.—Boundaries of areas I to XV referred to in the text. The dotted line represents the edge of the continental shelf.

fork (L.C.F.), and had for the most part reached breeding size. Blackburn and Gartner (1954) gave general information on size composition of catches and length at first maturity in Australian waters.

The following Section, II, is addressed especially to fisheries biologists concerned with *T. atun* or with the southern Australian region generally. Others may find it convenient to begin reading at Section II(*h*).

II. Diet: General Observations and Seasonal Changes

(*a*) *Southern Victoria*

Most of the Victorian catch of barracouta is made within 20 miles (generally much less) of the part of the coast from the South Australian border to Wilson's Promontory. Blackburn and Gartner (1954) distinguished four sections of this coastal strip, which they called areas IX, X, XI, and XII. These are shown in Figure 1, but for most purposes of this paper areas X, XI, and XII are considered together, as they are all part of the same large bight.

The barracouta of the whole region (areas IX, X, XI, and XII) are almost all members of the same population, which arrives on the coast and starts spawning in spring (September to November); remains there and continues spawning in summer (December to February); still remains there, although practically finished with spawning, in autumn (March to May); and leaves the coast in winter (June to August). In area IX there is frequently a minor winter visitation of a different winter-spawning population, which comes from South Australian waters (Blackburn and Gartner 1954).

The stomachs of 4590 fish of this region, 4156 from areas X, XI, and XII and the remainder from area IX, all taken between the end of 1948 and the beginning of 1955, were examined by scientific and technical staff at sea while the contents were fresh. They are classified according to their contents under the following headings:

(1) *Nil.*—The frequency of empty stomachs was high. A small number could have been included incorrectly in this class as a result of disgorging of food by the fish after capture, but this is not very common and would not necessarily empty the stomach.

(2) *Euphausiids.*—More stomachs contained this kind of food than any other. Only one species, *Nyctiphanes australis* Sars, has been recognized and it is unlikely that any other is available to a significant extent in this region; all euphausiids in the numerous plankton catches made in these waters have likewise proved to be *N. australis* (author, unpublished data), which fishermen call "brit" or "red feed".

(3) *Anchovy* (Engraulis australis (*White*)).—This small clupeoid fish is the second most common prey species of the barracouta in this region. It probably occurred more often than it was recorded, as some observers would not have been able to recognize it in a semi-digested state and would have recorded it as "fish remains" (see (8) below); the same applies to other fishes. Victorian fishermen have several names for this species, the commonest being "whitebait".

(4) *Juvenile barracouta.*—This was the third most common prey species. Individuals of up to 40 cm L.C.F. were obtained from the stomachs. Figure 2 shows the percentage of stomachs which contained this species in each month; it was small (not exceeding 2) in all months except April, when it reached 9, but this figure is probably abnormal (Section III(*a*)).

(5) *Pilchard* (Sardinops neopilchardus (*Steindachner*)).—This clupeoid species featured in the diet only in November and December and then in no more than 1 per cent. of stomachs. As it is freely eaten by barracouta in other Australian waters (see below, especially Section II(*f*)) it is probably not common on this part of the open coast of Victoria, a conclusion which is supported by other data (Blackburn 1950*c*).

(6) Trachurus *spp.*—*Trachurus* is a pelagic carangiform fish genus with two species in Victorian waters, *T. maccullochi* Nichols (*T. declivis* auct., non Jenyns) and *T. declivis* Jenyns (*T. novae-zelandiae* Richardson et auct.). The differences between them are small and it is generally impossible to identify part-digested specimens. Although *Trachurus* is a significant constituent of the diet of the barracouta in other Australian waters (Sections II(*d*) and II(*e*)) it was found in only one stomach from the southern Victorian coast and is therefore probably not common in that region.

(7) *Other identifiable fish.*—Other fish, in condition suitable for identification but not yet identified, were found in several months of the year but never in more than 1 per cent. of stomachs.

(8) *Fish remains.*—Remains of fish which the observers regarded as unidentifiable were consistently found in a small percentage of stomachs. The percentage did not exceed 3 in most months but was slightly higher (4–5) in spring and reached 8 in May. As the highest percentages occurred in months when anchovies were an important item of the diet it is highly probable that many of these remains were anchovies.

(9) *Cephalopods.*—These were found in only seven stomachs and appear to be unimportant in the diet. The species, which were mainly small squid, have not been identified.

(10) *Other crustaceans.*—Crustaceans other than euphausiids, which were mainly amphipods, were found in only seven stomachs. They have not been identified.

(11) *Mixed diet.*—Only 15 stomachs contained more than one kind of food. As many as three kinds (euphausiid, fish, and cephalopod) have been found in the same stomach.

Figure 2 shows for all available stomachs collected in each calendar month irrespective of year, the percentage containing: (*a*) no food, (*b*) euphausiids, (*c*) anchovy, (*d*) young barracouta, and (*e*) other foods (items (5)–(11) above, mainly fish remains).

In general the percentage of barracouta with stomach contents (feeding fish) rises from a minimum (11–12) in July and August, when the fish are scarcest, to a maximum (45–55) from November to February, and then falls during the autumn. The percentages in October and January, however, are considerably lower than those in the preceding and succeeding months.

Anchovy is virtually absent from the diet from January to April, but is a significant item in most other months. Blackburn (1950*a*) stated that the older anchovies in Victorian waters spend summer in shallow inlets and winter in the open

sea, although the younger individuals are mainly found in the inlets all the year round. As adult barracouta do not enter the inlets in force, anchovies would be available to them only during the sea phase. Figure 2 indicates that this is from May to December on this part of the Victorian coast. The very high percentage (32) of stomachs containing anchovy in November indicates that the species is most freely available to barracouta in that month; migration from the sea is probably then at its height, and there could be some associated formation of anchovy shoals as a preliminary to spawning, which occurs inside the inlets from late October onwards (Blackburn 1950*a*).*

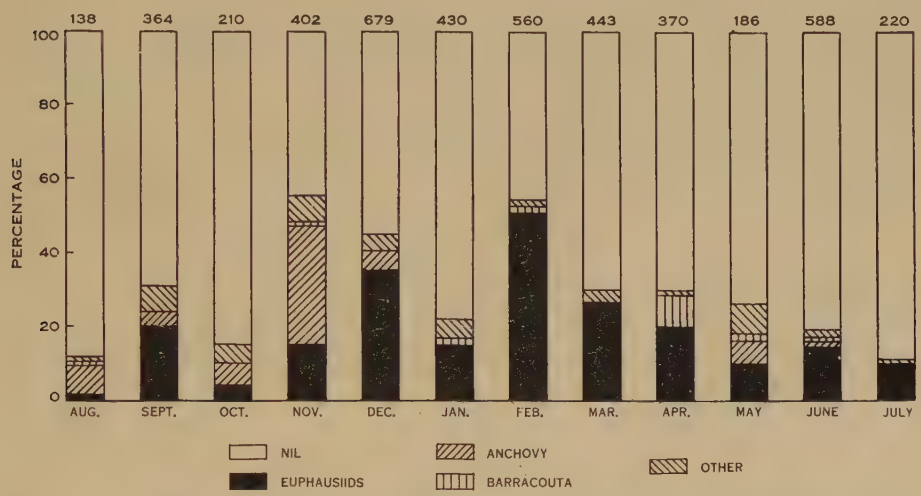

Fig. 2.—Percentage classification according to contents of barracouta stomachs taken each calendar month in areas IX, X, XI, and XII; material of different years combined. Numbers of stomachs are placed above the columns.

The percentage of stomachs containing euphausiids is at a minimum (1) in August, rises to 20 in September but is lower in the following two months, reaches 35 in December, falls in January, and reaches a maximum (51) in February; it then falls gradually back to the August minimum, although it is a little lower in May than in June. The general rise and fall in the consumption of *Nyctiphanes*, during the year, from a low level in the colder months to a high level in the warmer months and down again, reflects a corresponding change in the availability of the species in the upper layers of the sea (Sheard 1953). The subsidiary monthly variations in the percentage of stomachs containing *Nyctiphanes* (October, November, January, May) could be due to: (*a*) inadequate sampling, (*b*) preference of barracouta for other available food, (*c*) lessening of feeding by barracouta, or (*d*) real variations in the availability of

* Garner (1954) showed that surface temperatures in Port Phillip Bay are a few degrees higher from November to April, and a few degrees lower from May to September, than those in the adjacent part of Bass Strait; there is little difference in October. These periods correspond so well with the inlet and sea phases of the life of the older anchovy that they may indicate positive thermotaxis.

Nyctiphanes. The comparatively low November and May percentages might well be instances of (*b*), as anchovy was more prominent in the diet in those months than in the preceding and succeeding months, and is probably preferred by the barracouta to *Nyctiphanes* (Section II(*h*)). The October percentage could be an instance of (*a*). The low January percentage is probably an instance of (*d*), as it was evident in the data of both 1949–50 and 1950–51, when most of the summer material was obtained, and explanation (*b*) is inapplicable. There are no data to sustain explanation (*c*).

A significant point evident from Figure 2 is that from December to April, the middle and most of the later part of the normal barracouta fishing season, the fish is dependent upon *Nyctiphanes* for two-thirds or more of its food supply. Furthermore the supply of *Nyctiphanes* falls after February, when the barracouta, having completed spawning and preparing to migrate back to their winter quarters (Blackburn and Gartner 1954) are in need of food. It follows that the availability of fish from year to year at this period, in summer and especially in autumn, should be related to the availability of *Nyctiphanes*. Evidence of this is presented in Sections III(*a*) and IV.

(*b*) *Northern Tasmania*

Barracouta are caught commercially up to 20 miles (generally much less) from the northern coast of Tasmania. Blackburn and Gartner (1954) recognized three sections of this coastal strip which they called areas VI, VII, and VIII (Fig. 1), but these are considered all together in this paper.

The barracouta of the whole region are all members of the same population, which arrives on the coast, spawns, and departs at very much the same times of year and in very much the same way as the fish on the opposite side of Bass Strait, which were discussed above. In fact they are considered to belong to the same population as the southern Victorian fish (Blackburn and Gartner 1954) largely on account of these resemblances, although this hypothesis is not important to the argument of the present paper.

The number of barracouta stomachs examined from this region, which were all taken from the end of 1948 to the beginning of 1955, was 1468. Nearly all were obtained in November (251), March (251), and April (905). The November stomachs were 77 per cent. empty, 12 per cent. with anchovy, 3 per cent. with euphausiids, and 8 per cent. with other food, mainly unidentified fish remains which probably included anchovy. The March stomachs were 61 per cent. empty, 1 per cent. with anchovy, 36 per cent. with euphausiids, and 2 per cent. with other food. The April material was 69 per cent. empty, 17 per cent. with anchovy, 5 per cent. with euphausiids, 5 per cent. with young barracouta, and 4 per cent. with other food. Pilchard, *Trachurus*, and crustaceans other than euphausiids were not seen; cephalopods, other identifiable fish, and mixed food were found in only 11, 6, and 24 stomachs respectively. The euphausiids can be regarded as almost entirely *Nyctiphanes australis*, although another species, *Thysanoessa gregaria* Sars, has been encountered very occasionally in plankton catches from the northern Tasmanian region (author, unpublished data) and could be eaten by barracouta.

The diet of these northern Tasmanian barracouta in November and March is somewhat similar to that of southern Victorian fish (Section II(*a*)) in the same months: in both areas the anchovy is the most important item in November and *Nyctiphanes* is the only significant item in March. The April data are dissimilar for the two regions, anchovy being important in northern Tasmania and not in Victoria, and *Nyctiphanes* the reverse. But most of the April data for Tasmania were obtained in 1951, and if the April data of the two regions are compared for this particular year the difference in the percentage of stomachs with *Nyctiphanes* disappears, as it was low in both regions (see Section III(*a*)). The difference in percentage with anchovy, however, remains and indicates that the anchovy emerges from the inlets a month earlier in northern Tasmania than in Victoria, at least in some years. Blackburn (1950*a*) stated that the older anchovies of Tasmanian waters have similar sea and inlet phases of life, in the colder and warmer months respectively, to those in Victoria (see also Section II(*d*)).

Juvenile barracouta formed a significant part of the April diet on both the Victorian (Fig. 2) and Tasmanian sides of Bass Strait; but most of the records of this species refer to 1951 (Section III(*a*) and above), and it is probable that adult barracouta do not usually feed so heavily upon their young.

Since the observations on the feeding of barracouta in the two regions agree fairly well as far as they go, it is probable that the conclusion reached in Section II(*a*), about the dependence of the barracouta upon *Nyctiphanes* for its food in the summer and part of the autumn, is also applicable to northern Tasmania. It certainly is for the month of March.

(*c*) *King and Furneaux Islands*

These islands, respectively at the western and eastern ends of Bass Strait, were called areas VIII*A* and V respectively (Fig. 1) by Blackburn and Gartner (1954). Barracouta occur in both regions but are rarely fished commercially, and most of the material available for study was obtained by research vessels.

Only 280 stomachs, collected from 1948 to 1953, were available from King Island. Of these, 54 per cent. were empty, 28 per cent. contained euphausiids, 3 per cent. contained anchovy (all from April material), and 15 per cent. contained other foods, mostly unidentified fish remains. Pilchard, *Trachurus*, and young barracouta were not seen. The euphausiids were again *Nyctiphanes australis*, although *Thysanoessa gregaria* is occasionally found in the plankton of the area and could be eaten by barracouta. The data are insufficient for month-to-month comparison.

In the Furneaux Group 665 stomachs were collected between 1938 and 1953, the best-represented months being March (86), April (211), and June (174). The percentages of stomachs containing no food and euphausiids were respectively 57 and 35 in March, 54 and 44 in April, and 87 and 10 in June, which somewhat resemble those for the same months on the Victorian coast. The total of 665 stomachs were: 63 per cent. empty, 29 per cent. with euphausiids (again *Nyctiphanes*, although *Thysanoessa gregaria* occurs in the region and could be preyed upon), 1 per cent. with anchovy (all taken from March to May), and 7 per cent. with other foods, mainly

fish. Pilchard was not seen but *Trachurus* occurred in two stomachs, both in June (cf. Section II(*d*)). Barracouta occurred in one stomach. A juvenile Australian salmon (*Arripis trutta* (Bloch & Schneider)) was noted in one stomach obtained in June (cf. Section II(*d*)).

Even from these limited data it may reasonably be concluded that the barracouta of the Bass Strait islands, especially at the Furneaux Group in March and April, are at least as dependent on *Nyctiphanes* for their food as those in southern Victoria.

(*d*) *Eastern Tasmania*

There are important barracouta fisheries up to about 10 miles (generally less) from the eastern coast of Tasmania, where Blackburn and Gartner (1954) recognized four areas, I, II, III, and IV (Fig. 1).

The barracouta of the region as a whole are all members of the same population, which arrives on the coast in late spring (November) and remains until the end of autumn, spawning in late spring and early summer, and is not the same as the population of Bass Strait (Blackburn and Gartner 1954).

As almost all the available stomach material was collected in areas I, II, and III it is convenient to neglect area IV and consider the other three together. The number of stomachs is 2136, which were collected from 1938 (but mainly from 1949) to 1955. They are classified according to their contents as follows:

(1) *Nil.*—The frequency was high and is discussed below.

(2) *Euphausiids.*—This was the commonest kind of food observed. Only *Nyctiphanes australis* has been positively identified in the stomach contents but other species occur in the plankton of the Tasmanian east coast (continental shelf waters) and could have been confused with *Nyctiphanes* in stomachs by most of the observers. These are *Thysanoessa gregaria*, *Euphausia lucens* Hansen, *Euphausia similis* Sars var. *armata* Hansen, *Euphausia recurva* Hansen, *Nematoscelis* sp. (*megalops* Sars or *difficilis* Hansen), and *Stylocheiron* sp. *Thysanoessa* is the commonest of these minor species and all are very much scarcer than *Nyctiphanes* in this region (author, unpublished data).

(3) *Anchovy.*—As on the Victorian and Tasmanian coasts of Bass Strait, this was the second most common prey species identified.

(4) *Sprat* (Clupea bassensis *McCulloch*).—This small clupeoid fish, which is found only in Tasmania, was the third most common prey species identified. It occurred in 33 stomachs, all taken in January (Fig. 3), but it has frequently been seen in the stomachs of fishermen's barracouta catches in the autumn months, as late as May. Such catches (and shoals of sprats at the surface of the sea) are most common in semi-enclosed waters (Blackburn and Tubb 1950), but most of the 2136 stomachs considered here were obtained from the more open coastal waters, which accounts for the under-representation of sprat in them.

(5) Trachurus *sp.*—This occurred only in nine stomachs, all obtained from March to June, and accounted for up to 2 per cent. of the total material of those months. Although most specimens were part-digested they were probably all *T. declivis* Jenyns (*T. novae-zelandiae* auct.), as this species occurs in eastern Tasmanian waters at the same season and no other species of *Trachurus* has been satisfactorily recorded from Tasmania. *T. declivis*, called "horse mackerel", "jack mackerel", or more commonly "mackerel" in Tasmania, is so plentiful in south-eastern Tasmanian waters from January to June (Blackburn and Tubb 1950) that it was surprising to find so little of it in the material with which Figure 3 deals. In earlier years (e.g. 1943) it was sometimes very common in the stomachs of barracouta caught by commercial fishermen, and may have been more plentiful at that time. *T. declivis* grows to about 45 cm but is probably unutilizable by barracouta at sizes over about 30 cm.

(6) *Juvenile barracouta.*—These were much less frequent in the diet than in Bass Strait, being found in only three stomachs, although juveniles of suitable size are often found in the eastern Tasmanian region.

(7) *Pilchard.*—This species occurred in a very few stomachs obtained from January to July in the period 1941–1945, but was not seen in the much larger material of the period 1949–1955. It is not common in the region (Blackburn 1950*c*).

(8) *Australian salmon.*—Juveniles occurred in three stomachs in March and April. At sizes over about 30 cm it is unlikely that it could be taken by barracouta.

(9) *Other identifiable fish.*—These occurred in only three stomachs.

(10) *Fish remains.*—Part-digested fish which the observers regarded as unidentifiable occurred in 30, 20, and 16 per cent. of stomachs obtained in December, January, and June respectively. As these were also the months in which barracouta fed most heavily on anchovy (Fig. 3, and below) it is highly probable that many of these fish remains were of that species.

(11) *Cephalopods.*—Unidentified cephalopods, mainly small squid, occurred in only 13 stomachs.

(12) *Other crustaceans.*—Stomatopod larvae were observed in the stomach of one fish.

(13) *Mixed diet.*—Only in 18 stomachs was there a mixture of prey.

Thus the diet of barracouta in this region is slightly more varied than in Bass Strait, but *Nyctiphanes* and anchovy are still the most important constituents.

Figure 3 shows the percentages of stomachs containing: (*a*) no food, (*b*) euphausiids, (*c*) anchovy, (*d*) sprat, and (*e*) other foods (items (5)-(13) above, mainly fish remains) in each month. Only 23 stomachs were collected in the months July to October, when barracouta are extremely scarce in the region, and these are neglected in Figure 3; 14 contained euphausiids and 9 were empty.

The percentage of feeding fish as shown by these data rises from 14 in November to 75 in January, falls sharply to 13 in March, and rises to 63 in June.

This variation from month to month is partly due to changes in the availability of anchovy and variation in the amount recorded as "fish remains". Anchovy is virtually absent from the diet from February to April, but a significant item in most other months and a large one in January and June. This situation, similar to that found on the Victorian coast of Bass Strait, is a result of the two-phase (sea and inlet) annual cycle of the anchovy referred to in Sections II(*a*) and II(*b*).

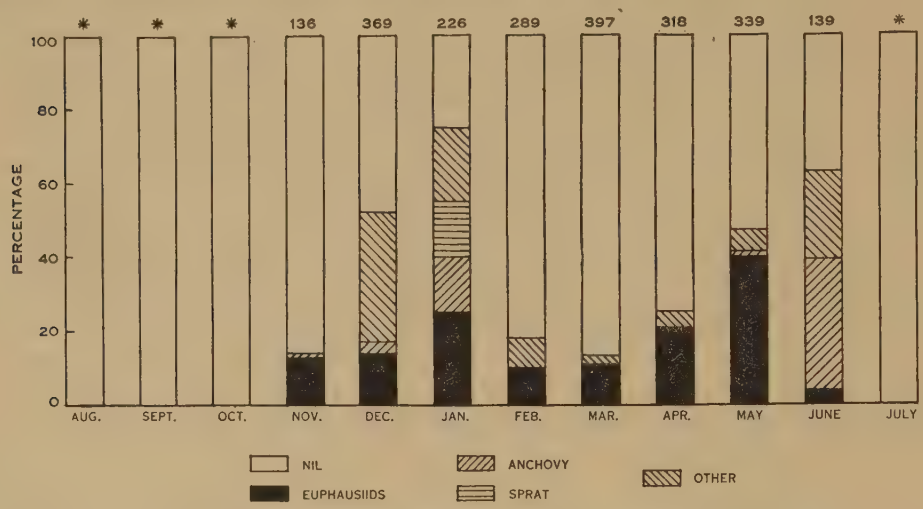

Fig. 3.—Percentage classification according to contents of barracouta stomachs taken each calendar month in areas I, II, and III; material of different years combined. Numbers of stomachs, which were nil or negligible for certain months (*), are placed above the columns.

There are also two well-separated maxima in the consumption of euphausiids (mostly *Nyctiphanes* in all months) by barracouta, which is not the case in Victorian waters. The first occurs in January (25 per cent. of stomachs) and the second in May (40 per cent.). This is so well marked that it is unlikely to be due to inadequate sampling, but there are, as yet, insufficient data from plankton studies to confirm or deny that there are two such maxima in the actual availability of *Nyctiphanes* in the region. In 1951 the consumption of *Nyctiphanes* was much heavier in May than in April in the same locality (area III).

From February to April the barracouta is sparsely supplied with food and dependent upon *Nyctiphanes* for most of the food it obtains. In May its main food is likewise *Nyctiphanes*, although the supply is larger. The availability of barracouta in these months should therefore be related to the availability of *Nyctiphanes* in the same way as in southern Victoria at about the same time of year. Some data bearing upon this point are presented in Sections III(*b*) and IV.

The available data from western Tasmania are insignificant.

(*e*) *Eastern Victoria and New South Wales*

There are significant coastal barracouta fisheries at Lakes Entrance, Vic., and Eden, N.S.W., in what Blackburn and Gartner (1954) named areas XIV and XV respectively (Fig. 1). The barracouta of these two areas are all members of the same

population, which occurs at Lakes Entrance from May to August and occasionally from November to February, and at Eden in all months from May to January, spawning from May to November (Blackburn and Gartner 1954).

Almost all the available stomachs from Lakes Entrance and other Victorian localities in area XIV were taken in 1949 and 1950 in July and August (416 stomachs of a total of 432, the others being obtained in March and November). The July and August fish were feeding well, as shown by the following percentage classification of stomachs: 31 per cent. empty, 41 per cent. with anchovy, 25 per cent. with sandy sprat (*Hyperlophus vittatus* (Castelnau), a small clupeoid fish), 2 per cent. with pilchard, and 1 per cent. with other foods (including *Trachurus* sp. and squid, each in one stomach only); there were no euphausiids. These occurrences of anchovy, sandy sprat, and pilchard have been discussed elsewhere (Blackburn 1950*a*, 1950*c*); the anchovy enters the inlets in spring and remains there until autumn, when it reappears at sea (cf. Sections II(*a*), II(*b*), and II(*d*) of this paper); the sandy sprat behaves like the anchovy but the pilchard remains at sea throughout.

Only 167 stomachs were collected at Eden and other places in southern New South Wales: 40 in July (1953), 114 in November (mostly 1948 and 1953), and 13 in other months. The July stomachs were 55 per cent. empty, 22 per cent. with *Trachurus*, and 23 per cent. with other foods, mainly fish remains and not including euphausiids. Those taken in November were 44 per cent. empty, 14 per cent. with euphausiids, 10 per cent. with *Trachurus*, 3 per cent. each with anchovy and pilchard, and 26 per cent. with other foods, mainly unidentified fish remains (squid and barracouta each in one stomach only).

Nyctiphanes australis is the commonest euphausiid in the southern New South Wales coastal area and was identified in many of the stomach contents, but the following other species were found in a few barracouta taken 8–18 miles off the coast (beyond the normal range of the fishery) in the month of October: *Thysanoessa gregaria*, *Nematoscelis* sp. (*megalops* or *difficilis*), and *Euphausia recurva*. Other euphausiids occasionally recorded in plankton catches on the continental shelf of southern New South Wales are *Euphausia similis similis* Sars, *Pseudeuphausia latifrons* (Sars), and *Stylocheiron* sp. (author, unpublished data). The absence of *Nyctiphanes* in stomachs so far obtained in areas XIV and XV in the winter months is in agreement with other information about the seasonal distribution of this species in surface waters in the south-eastern Australian region (Sheard 1953, and Section II(*a*) of this paper).

The *Trachurus* in the July and November stomachs from New South Wales were part-digested and could have been either *T. declivis* or *T. maccullochi*, since both occur in the area, where they are called "cowanyoung" and "yellowtail" respectively. Blackburn and Rayner (1951) referred to the abundance of shoals of the former species near Eden between July and November. The occurrence of anchovies in this area in November is in line with previous records from August to February (Blackburn 1950*a*), but little is known about the life history. As for the pilchards, Blackburn and Tubb (1950) have shown that these occur at two separate seasons in southern New South Wales waters, one from February to June (for adult fish) and one from September to December (mainly for yearlings), which explains their appearance in the November barracouta stomachs and their absence from those of July. Had

stomachs been collected in May or June, the early part of the barracouta season in this area, the presence of pilchards would have been expected. The pilchard is much commoner in this and the eastern Victorian region than in southern Victorian and Tasmanian waters (Blackburn 1950*c*; Blackburn and Tubb 1950).

(*f*) *South Australia and Western Australia*

A moderate amount of material was collected in the coastal waters of these States, along the south coast of the Australian mainland from long. 141° E. (the western border of Victoria) to long. 118° E. (the vicinity of Albany, W.A., the approximate western boundary of the barracouta as a common species in Australian waters). There is no commercial fishing for the species in these waters.

In eastern South Australian waters (long. 137° 30′ to 141° E., area XVI of Blackburn and Gartner (1954)) 209 barracouta stomachs were collected, nearly all in March (1939 and 1953), when the classification according to stomach contents was: 37 per cent. empty, 44 per cent. with euphausiids, 6 per cent. with anchovy (post-larval), 4 per cent. with pilchard, 1 per cent. with squid, and 8 per cent. with other foods, mostly fish remains (no barracouta or *Trachurus*). The barracouta which occur in this area at this season are thought to belong to the same population as the southern Victorian and northern Tasmanian fish (Blackburn and Gartner 1954).

The number of stomachs available from the western part of South Australia (long. 129° to 137° 30′ E.) is 146, nearly all for the months of April (1947, 1949, and 1953) and May (1949) when the classification was: 68 per cent. empty, 19 per cent. with pilchard, 4 per cent. with euphausiids, 2 per cent. with ruff (*Arripis georgianus* (Cuvier & Valenciennes), a small semi-pelagic coastal fish which is commoner in South and Western Australia than further east), and 7 per cent. with other foods, including anchovy and barracouta each in one stomach only, but no *Trachurus*. The barracouta of this part of South Australia are a different population from any previously discussed; they spawn in late autumn and winter (Blackburn and Gartner 1954).

The euphausiids were *Nyctiphanes australis*, which is the only species so far recorded in the neritic waters of South Australia. Its western known limit of distribution is in long. 132° E. (author, unpublished data).

The anchovy records agree with other data from the region, but little is known about the life history of this species there (Blackburn 1950*a*). The pilchard is known to be abundant in South Australian waters in the autumn, much more so than in Victorian or Tasmanian waters at any season (Blackburn 1950*c*). *Trachurus declivis* and *T. maccullochi* both occur in South Australia (Waite 1923) although they have not yet been found in barracouta stomachs.

On the south coast of Western Australia (long. 118° to 129° E.) only 88 stomachs have been obtained, all in May, June, and July (1947 and 1951). This is the season of spawning and greatest availability in the coastal waters. The stomachs were 78 per cent. empty, 15 per cent. with pilchard (common in the area at that season; see Blackburn 1950*c*), and 7 per cent. with other food, including ruff in one stomach only, but no euphausiids, anchovy, barracouta, or *Trachurus*. However, Whitley (1946)

found anchovy, *Trachurus declivis*, and the true mackerel *Scomber australasicus* Cuvier & Valenciennes in the stomachs of barracouta taken in this area in June. Euphausiids generally are much scarcer in the area than in the other regions previously discussed, and *Nyctiphanes australis* is altogether absent.

(*g*) *Overseas*

A good qualitative account of the diet of barracouta at Otago, New Zealand, was given by Graham (1938) who identified almost every species of prey from between 400 and 500 stomachs. He listed 9 species of fish, 8 of crustaceans (including some benthic forms), 1 annelid, and "squid". Unfortunately, Graham did not state the order of importance of these species in the diet, but elsewhere (1953) he indicated that pilchard (*Sardinops neopilchardus*), sprat (*Clupea antipodum* Hector, a close relative of the Tasmanian *C. bassensis*), and ahuru (*Auchenoceros punctatus* (Hutton), a small gadoid fish unknown in Australia) are the species most commonly taken. *Nyctiphanes australis* was simply mentioned among the crustaceans. Juvenile barracouta were not recorded.

At St. Paul and Amsterdam Is. in the south Indian Ocean *Thyrsites atun* feeds on several species of fishes and larval stages of crustaceans (Angot 1951) but no list has been given.

In South Africa the species feeds chiefly on pilchards (*Sardinops ocellata* (Pappe), a close relative of the Australian and New Zealand pilchard) but also takes maasbanker (*Trachurus trachurus* (Linnaeus)), mackerel (*Scomber japonicus* Houttyn), anchovy (*Engraulis japonicus* (Houttyn)), harder (mullet, various Mugilidae), and other small fishes (Barnard 1947; Davies 1954). A euphausiid, *Nyctiphanes capensis* Hansen, has also been found in the diet of *Thyrsites atun* in this region (Boden 1955), but according to personal communications from South African investigators euphausiids are rarely taken by this species, although they are common in parts of the region and are utilized by other fishes (Davies 1949).

Nothing has been published about the diet of *Thyrsites* at Tristan da Cunha in the south Atlantic Ocean. Off the Atlantic coast of Patagonia it has been found to feed on *Clupea fuegensis* (Jenyns) and a small flatfish, *Thysanopsetta naresi* Günther (Hart 1946). For the coast of southern Chile the only published information is that of Bahamonde (1951) who examined 25 stomachs, most of which were obtained in December, January, and February. There were 2 empty stomachs, 5 with euphausiids only, 9 with fish (mainly "sardinas") only, 1 with another crustacean (*Munida*) only, and 8 with mixed food, including polychaets and cephalopods.

(*h*) *Remarks*

The preceding observations present the barracouta as a feeder on almost every type of available small nekton, especially schooling fishes; on a few kinds of plankton, mainly euphausiids; and to a less extent on some kinds of benthos or seston (Graham 1938; Bahamonde 1951), which may be found to be more important in the diet when more is known about subsurface occurrences of the fish (Blackburn and Gartner 1954).

The main items in the diet of the barracouta in the two best-studied regions, southern Victoria and eastern Tasmania (which are further discussed in Sections III, IV, and V), are the euphausiid *Nyctiphanes australis* and the fish *Engraulis australis* (anchovy). The anchovy has a period of inlet residence which makes it unavailable during much of summer and autumn to the barracouta, which is then dependent upon *Nyctiphanes* for most of its food supply: at other times of the year both species are consumed.

Graham (1953) expressed surprise that a fish with such powerfully armed jaws should feed at all on plankton. The virtual absence of gillrakers seems further to unfit it for this role. Its method of feeding was once observed in clear shallow water by a former colleague of the author, Mr. J. A. Tubb. A number of barracouta, in the presence of a diffuse swarm of *Nyctiphanes australis*, swam round and round herding them into a tightly packed mass, which they then attacked open-mouthed. It would not always be necessary for the fish to herd the prey, as *Nyctiphanes* sometimes occurs naturally in large densely-packed concentrations or "rafts" (Sheard 1953) which are often attended by barracouta and other predators. However, it is unlikely that the fish could utilize very sparse and scattered occurrences of *Nyctiphanes* (e.g. one or two per cubic metre of water) in the way described above or in any other, and the occurrence of *Nyctiphanes* in the stomach of a barracouta probably indicates that the fish has encountered it in high concentrations. *Nyctiphanes australis* does not exceed 14 mm in total length (Sheard 1953) and it is most improbable that it is eaten singly.

Despite its surprising efficiency as a predator of *Nyctiphanes* the barracouta is structurally better fitted for the capture of fish, which it may take in preference to *Nyctiphanes* when both are available, although this is not certain; there can be no clear preference for *Nyctiphanes* over fish, however, or the fish-like lures which the fishermen use on their troll lines and poles would be useless when *Nyctiphanes* was abundant.

The fish diet of the barracouta at any particular time and place in Australian waters reflects the availability of small pelagic fish as ascertained in previous work. This was shown in Sections II(*a*) to II(*f*). For instance, the stomach contents suggest that Bass Strait has fewer such species in abundance than adjacent neritic waters to the north, south, and west, and this was well known previously; and the species which are known to inhabit a particular area at a certain season are found in barracouta stomachs in approximately the expected proportions, and appear in and disappear from the diet at about the expected times.

However, the barracouta does not utilize every available food resource within its area of occurrence. Only in negligible numbers do the adult fish enter such inlets as Port Phillip Bay, Vic. (Fig. 1), to prey upon the anchovies and pilchards which are often abundant there, although juvenile barracouta are commonly found feeding in those waters. And in winter and early spring, when anchovies are common in the open waters of Bass Strait and the east coast of Tasmania, and shoals of whitebait (*Lovettia seali* (Johnston), a small salmonoid; Blackburn 1950*b*) are entering the rivers of northern and south-eastern Tasmania, barracouta are seldom there. Further, when barracouta occur off Eden, N.S.W., in winter and spring, being then as far north as they occur as a common species on the east coast of Australia, they meet only the

fringe of a large winter occurrence of pilchards which extends nearly a thousand miles further north; the barracouta actually is found over most of that range, but not commonly and with increasing rarity towards the north (Blackburn and Gartner 1954).

That is to say, the distribution of the barracouta as a plentiful species is not determined merely by abundance of suitable food under physical conditions which it can tolerate. It probably prefers a narrower range of physical conditions such as temperature and salinity and is distributed accordingly, provided that some suitable food is available; a preferred temperature range of 13–18°C has already been indicated, although the species can tolerate temperatures as low as 9° or 10° and as high as 19° or 20° (Blackburn and Gartner 1954). The lowest chlorinity on record in an area containing barracouta is 5·7 parts per thousand (Blackburn 1950*b*, p. 160). The vagaries of distribution within regions where the preferred physical conditions prevail pose a different problem, on which some light is thrown subsequently.

III. Diet: Annual Changes in Coastal Fish

(*a*) *Southern Victoria*

Figure 4 presents a dissection of most of the data of Figure 2 (those from areas X, XI, and XII, i.e. the bight on the Victorian south coast) according to different years. Comparisons between diets in those years can most validly be made for the summer quarter (December to February), the data for the autumn quarter (March to May) being the next best. As noted in Section II(*a*), these are the periods when the barracouta depends upon the euphausiid *Nyctiphanes australis* for most of its food supply.

Food, mainly *Nyctiphanes*, appears to have been less plentiful in the summer of 1949–50 than in that of 1948–49 and much less plentiful again in each of the succeeding two summers. There are no data for the summer of 1952–53, but by 1953–54 the consumption of food was again as high as that of 1949–50.

For the autumn quarter there are data for four years only, 1949–50 through 1952–53, and fewer observations per year than in the summer quarter. *Nyctiphanes* appears to have been scarcer in 1950–51 and 1951–52 than in 1949–50 and 1952–53, when it featured in the diet to the same moderate extent. Figure 4 suggests that the barracouta made up the deficiency of *Nyctiphanes* by feeding more on other organisms in 1950–51 and 1951–52, but it is doubtful whether they did. The food resorted to in the autumn of 1951 was juvenile barracouta, but actually this was noted only in April, when it also occurred in 5 per cent. of northern Tasmanian stomachs (Section II(*b*)). It is possible that young barracouta were more freely available than usual in Bass Strait that month, or even all autumn, but it is unlikely that they could so enormously have outnumbered the adults as to provide them with sufficient food for 2 or 3 months. As for the anchovy and other non-euphausiid food noted in stomachs in the autumn of 1952, this was only in May, when such food normally becomes available (Fig. 2); little food was found in stomachs in March or April.

It should be pointed out that area X supplied a smaller proportion of the available data in 1951–52 than in the other years. Only 37 stomachs were collected in area X in the summer and autumn of 1951–52, and these were all in May.

With this reservation, which will be mentioned in Section V, it may be concluded that *Nyctiphanes* was scarcer in the summer and autumn diet of barracouta in 1950–51 and 1951–52 than in the two preceding and succeeding years in the bight on the south coast of Victoria, and was not replaced to any appreciable extent by other kinds of food except in May (and possibly in April 1951). That is to say, *Nyctiphanes*, in

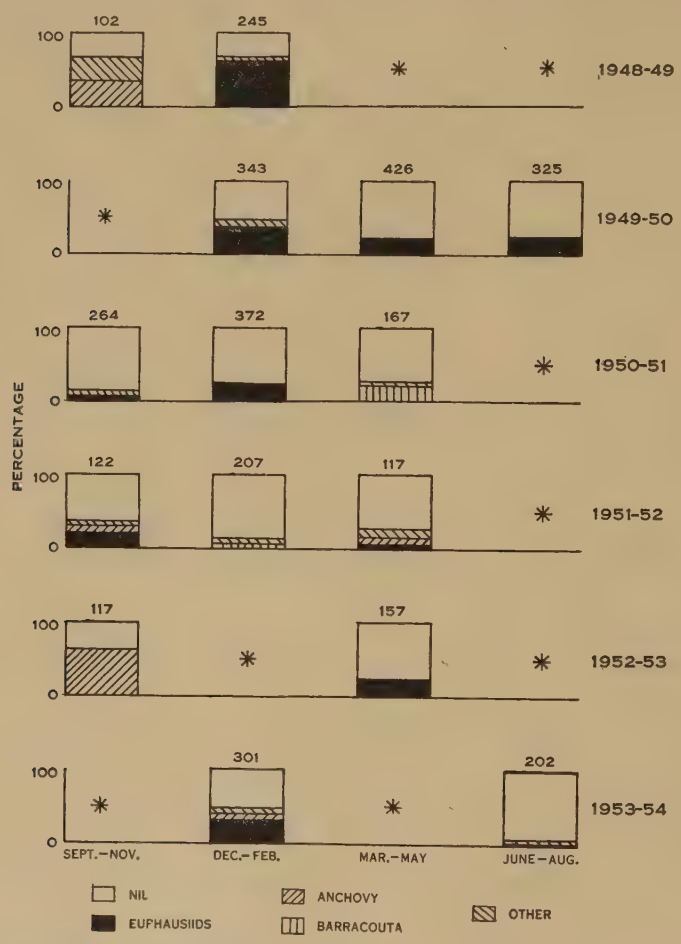

Fig. 4.—Percentage classification according to contents of barracouta stomachs taken each quarter of each year from 1948–49 through 1953–54 in areas X, XI, and XII. Numbers of stomachs, which were nil or negligible for certain quarters (*), are placed above the columns.

concentrations sufficiently dense for barracouta to utilize, was probably scarcer than usual for the time of year in those waters in those two years, and the fish had less food than usual while they were there. Observations on plankton collections are not helpful because the hauls in and before 1950–51 were made in the day-time, when *Nyctiphanes* is generally scarce in the water layers which were sampled, and there were no hauls in 1951–52.

Small differences in percentages such as these are of such limited reliability that it is impossible to decide which of the two years 1950–51 and 1951–52 was the poorer as regards availability of *Nyctiphanes*. All that may reasonably be concluded is that both were poor in this respect during summer and autumn.

The data for the spring quarter (September to November) of 1950–51 suggest that anchovies were scarcer than usual and that barracouta were therefore short of food.

The meagre data for the winter quarter are nearly all for the month of June, which is usually the end of the barracouta season on this coast. The percentage of stomachs containing food (*Nyctiphanes*) was as high for June 1950 as for the preceding quarter, which is unusual (Fig. 2). Recorded sea temperatures were abnormally high in the region that winter, not falling much below 13°C (Blackburn and Gartner 1954).

(*b*) *Eastern Tasmania*

When the data of Figure 3 are reassembled according to the spring, summer, autumn, and winter quarters of different years the only important feature is a series of percentages for five successive autumns (March to May), 1948–49 through 1952–53. The numbers of stomachs collected in these autumns are respectively 172, 232, 256, 147, and 153; the percentages of stomachs containing any food were 62, 19, 20, 11, and 4; and the percentages of stomachs containing euphausiids were 55, 16, 17, 8, and 4. Good data for the summer quarter are available only for 1948–49, 1951–52, and 1952–53, the numbers of stomachs being respectively 113, 287, and 254; percentages with food were respectively 82, 15, and 39, and percentages with euphausiids 49, 10, and 3. As far as they are available the summer percentages of stomachs containing euphausiids are close to the corresponding percentages for the autumns of those years, although non-euphausiid food is much more important in the summer months, as is also shown in Figure 3. The percentages for 1948–49 may not be comparable with those of the later years because the summer stomachs of that year were nearly all taken in January and the autumn stomachs nearly all in May, these being the two months in which feeding on euphausiids is particularly heavy. There are no useful data for the spring or winter quarters of different years, and none at all for 1953–54.

These data indicate a gradual decline in the consumption of euphausiids (mainly *Nyctiphanes*) from year to year from 1949–50 (and possibly from 1948–49) to 1952–53, in autumn and possibly also in summer, with no other food taking its place in autumn. This may be contrasted with a fall and subsequent recovery in consumption of euphausiids over the same period of years at the same seasons of year on the south coast of Victoria (Section III(*a*)). It is reasonable to interpret these annual variations in the consumption of *Nyctiphanes* in autumn, when the barracouta is practically restricted to that food, as evidence of corresponding variations in the autumn availability of *Nyctiphanes* in the sea in concentrations which barracouta could utilize. Useful data from plankton collections are not available for either region.

IV. Fluctuations in Availability of Coastal Fish

Blackburn and Gartner (1954) discussed recent changes in the abundance of barracouta, as measured by catch per unit of fishing effort (total catch divided by number of boat-months), in the coastal fishing areas of Victoria and Tasmania up to the end of 1951–52. They pointed out that the most marked changes had occurred in the Bass Strait population (i.e. on the south coast of Victoria and the north coast of Tasmania) where there was more reason to ascribe them to changes in availability of the population to fishermen than to changes in actual abundance in the population as a whole. With catch and effort data now to hand for two more years some further comment may be made.

Table 1 presents catch and effort totals, for each of the years for which trustworthy information is available, for barracouta of the Bass Strait and eastern Tasmanian populations. For practical purposes all catches in areas IX, X, XI, and XII on the south coast of Victoria and areas VI, VII, and VIII on the north coast of Tasmania are referable to the Bass Strait population and all catches in areas I, II, III, and IV to the eastern Tasmanian population (Fig. 1). Full details of the sources of catch and effort data were given by Blackburn and Gartner (1954).

Although the catch per boat-month is at present the best measure of availability of fish it has its imperfections. For example, the amount of fishing time available during a given month depends upon weather conditions, since most of the boats are small. Another point which deserves special mention is the fact of cooperation (largely involuntary) between different crews in the same area in the search for fish, so that a large fleet is apt to fish more efficiently than a small one.

Table 1(*a*) (Bass Strait) shows the fall in catch per unit effort in 1950–51 in areas X, XI, and XII and areas VI, VII, and VIII, which was referred to by Blackburn and Gartner (1954). During the next three years the catch per unit effort was approximately normal in areas X, XI, and XII (combined) but not so on the Tasmanian side of Bass Strait, where it fell further. In the Victorian area IX, for which effort data are not available for years preceding 1950–51, there was first an increase and then a decrease in catch per unit effort after that year. In eastern Tasmania (Table 1(*b*)), the catch per unit effort was fairly stable from year to year until it fell very low in 1953–54; a minor fall had occurred 2 years before, as noted by Blackburn and Gartner (1954).

Much more information is obtainable by dissecting the annual catch, effort, and catch per unit effort records according to portions of the year. Blackburn and Gartner (1954) did this for months and half-years, but for the purpose of this paper it is most convenient to consider the different quarters of the year—spring, summer, autumn, winter, as defined in Section III(*a*)—as is done in Figure 5. This shows the mean catch per boat-month, which is a measure of abundance of fish in the fishing areas (availability to the fisherman), for each quarter for each area or group of areas listed in Table 1.

Abundance tends to vary within the year in a way which is fairly characteristic for each region. In area IX and areas X, XI, and XII abundance in the summer quarter is generally lower than that in either spring or autumn; in areas VI, VII,

and VIII abundance is generally much lower in both spring and summer than in autumn; while in areas I, II, and III, and in area IV, it is generally much greater in both summer and autumn than in spring. There are exceptions. These differences, which reflect different times, paths, and other circumstances of the coastwise migrations and return migrations of the barracouta populations, were discussed in some detail by Blackburn and Gartner (1954).

TABLE 1

RECORDED CATCH OF CLEANED HEADLESS FISH (*C*, IN THOUSANDS OF LB), FISHING EFFORT (*E*, IN BOAT-MONTHS), AND CATCH PER UNIT FISHING EFFORT (*C*/*E*), FOR DIFFERENT AREAS OF OCCURRENCE OF THE BASS STRAIT AND EASTERN TASMANIAN BARRACOUTA POPULATIONS

(*a*) *Bass Strait**

Year	Area IX†			Areas X, XI, XII†			Areas VI, VII, VIII‡			Total		
	C	*E*	*C*/*E*	*C*	*E*	*C*/*E*	*C*	*E*	*C*/*E*	*C*	*E*	*C*/*E*
1947–48	517	?	?	4766	?	?	4217	1160	3·6	9500	?	?
1948–49	440	?	?	4889	1156	4·2	4990	1443	3·5	10318	?	?
1949–50	384	?	?	4082	975	4·2	2210	639	3·5	6675	?	?
1950–51	449	248	1·8	2503	896	2·8	646	360	1·8	3599	1504	2·4
1951–52	543	224	2·4	2885	725	4·0	1088	511	2·1	4516	1460	3·1
1952–53	510	270	1·9	3292	880	3·7	190	148	1·3	3992	1298	3·1
1953–54	122	109	1·1	3454	886	3·9	45	46	1·0	3621	1041	3·5

(*b*) *Eastern Tasmania*

Year	Area IV			Areas I, II, III			Total		
	C	*E*	*C*/*E*	*C*	*E*	*C*/*E*	*C*	*E*	*C*/*E*
1947–48	358	122	2·9	2487	558	4·5	2845	680	4·1
1948–49	184	122	1·5	2842	518	5·5	3026	640	4·7
1949–50	171	106	1·6	2022	329	6·1	2193	435	5·0
1950–51	367	118	3·1	2204	418	5·3	2571	536	4·8
1951–52	141	123	1·1	1230	411	3·0	1371	534	2·6
1952–53	183	125	1·5	2391	481	5·0	2573	606	4·2
1953–54	58	61	1·0	483	239	2·0	541	300	1·8

* Excluding Victorian areas XIII and XIV and Tasmanian areas V and VIII*A* (Fig. 1).

† Victorian south coast.

‡ Tasmanian north coast.

Abundance in the winter quarter is virtually the abundance in June only, as barracouta are generally very scarce in all these areas in July and August and little fishing is then done. This explains the high variability from year to year in these winter indices compared with the others, most of which depict the average abundance over a period of 2 or (usually) 3 months. Where the winter catch per boat-month

exceeds 2000 lb it always follows a good autumn's fishing and may be regarded as an extension of that. Exceptionally great abundance of barracouta in the winter quarter occurred in areas X, XI, and XII in 1950 (actually only in areas X and XI; see Blackburn and Gartner 1954, Fig. 13) when fish were not only very plentiful in June but almost as much so in July, and were even fairly abundant in August in area XI; sea temperatures were higher than normal that winter, and *Nyctiphanes* more abundant than usual for the time of year (Section III(*a*), this paper).

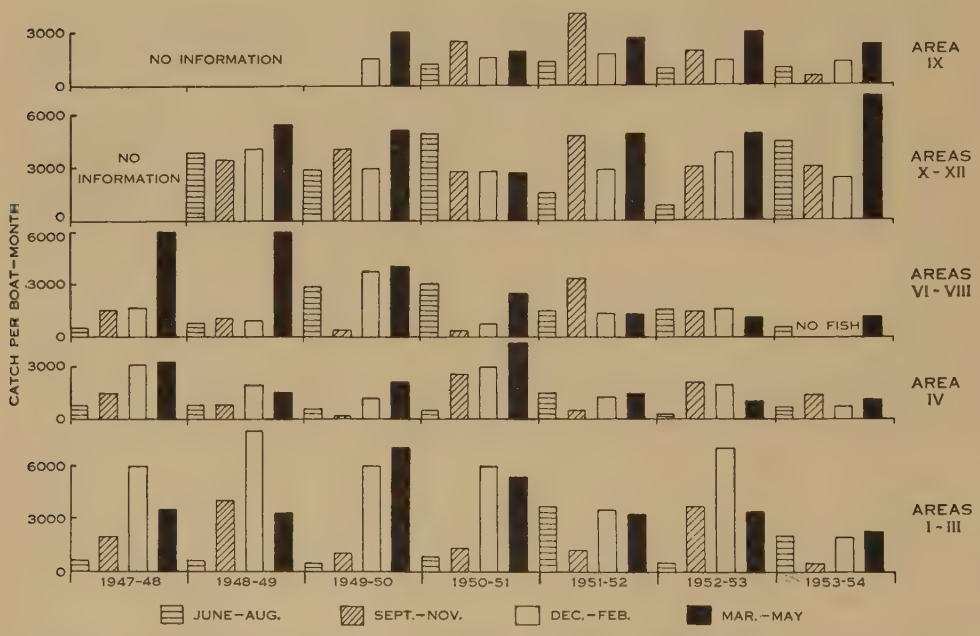

Fig. 5.—Mean catch per boat-month (lb) of barracouta in each quarter of each year from 1947–48 to 1953–54, for each of the areas and groups of areas shown on the right.

The data for the spring quarter in areas I, II, III, and IV likewise relate virtually to a single month, November, and they too are very variable; but on the whole the abundance of fish at that time is low, and when it is not it is generally the forerunner of a good summer's fishing and may be regarded as an early commencement of that.

The rest of the data may be examined region by region, starting with areas X, XI, and XII combined. Figure 5 shows that abundance varies a little less from year to year in spring than in summer and much less than in autumn: the spring maxima and minima are 4740 and 2700 lb per boat-month (1·76:1·00); those for the summer are 4120 and 2320 (1·78:1·00); while for the autumn quarter the corresponding figures are 7040 and 2620 (2·69:1·00). Further, abundance in spring varies in an apparently erratic manner from year to year, e.g. the worst spring (1950) being followed by the best (1951). But abundance in the six autumns reveals a regular trend from a high level in 1949 to a minimum in 1951 and recovery to a maximum in 1954, resembling

the trend in abundance (mean catch per boat-month) for the year as a whole (Table 1); and the summer data show a similar trend, except for the last year of the series (1953–54).

The autumn almost always yields a much greater total catch than either the spring or summer in this region (Blackburn and Gartner 1954).

That is to say, the degree of success or failure of the fishery in a given year depends mainly on how abundant the fish were in summer and especially in autumn, and to a much less extent on the abundance in spring; the latter varies comparatively little from year to year, in a manner which is apparently unrelated to the variations in abundance in the summer and autumn, although the fish available in the catch of these seasons all belong to the same migrating population. And although the summer abundance indices exhibit much the same trends from year to year as the autumn and whole-year indices, they do so much less clearly; the range of variation is narrower and the annual fluctuations are damped.

Such changes obviously cannot be ascribed entirely to natural (or man-made) fluctuations in the size of the population as a whole. They must have been, in large measure if not entirely, effects of natural fluctuations in availability of parts of the population: that is to say, changes in distribution or behaviour of those parts causing them to be more or less freely catchable by coastal fishermen, who wait for these migratory fish and are able to catch them only when they are near the surface. Since the spring and summer are the spawning periods, when the population would probably be less dispersed than later in the season, catch per unit effort in these periods, from year to year, should represent the actual size of the population more faithfully than the corresponding index in autumn. It follows that if changes in abundance (population size) and changes in availability (population distribution or behaviour) both affect the fishery, the effect of the former should be maximal in the spring and summer; but as it is precisely at those seasons that year-to-year variation in fishing success is least, it may be concluded that changes in availability, operating mainly in autumn, have the greater effect. It is not certain that changes in abundance have had any effect.

It might be thought that the uniform and rather low level of catch per unit effort through the spring, summer, and autumn of 1950–51, the poor year of the series, should be interpreted as a reduction in the size of the population as a whole (Fig. 5). The succession of events between the summers of 1949–50 and 1951–52 was: a good autumn, the best recorded winter, the worst recorded but by no means disastrous spring, a fair summer, an extremely bad autumn, a bad winter, and the best spring on record. Subsequent catches were also good. Fluctuations in population size, in fish with several year classes in the exploited portion of the population, do not usually pass so quickly, but if there had been one at this time the mean catch per unit effort of the summer of 1950–51 should have been lower. Effects of availability could have operated separately in spring and autumn, a possibility which is discussed in Section V.

The succession of events in area IX, for the $4\frac{1}{2}$ years for which catch per unit effort data are available, parallel those in areas X, XI, and XII, as would be expected; except for 1953–54, when fishing was worse instead of better than in the previous

year in all seasons, a point which is discussed in Section V. Two notable points of correspondence with the series just discussed are the bad autumn and particularly good spring of 1951. The spring of 1950 was better here than the following summer and autumn, which supports the abovementioned hypothesis that the low catch per unit effort in the same period in areas X, XI, and XII was an effect of local availability.

The data for areas VI, VII, and VIII, on the opposite side of Bass Strait, somewhat resemble those just discussed up to the summer of 1951–52: for instance, there was the same decline in the catch per unit effort from autumn to autumn (the most important season), and the same unusually good catch per unit effort in the spring (generally a very poor quarter in this region) of 1951. However, there was no worth-while fishing after the spring of 1951: abundance in the autumn declined further, instead of recovering as it did on the Victorian coast, and abundance in spring and summer was low (although not abnormally so) in 1952–53, and virtually nil (although only three boats fished) in the following year. These changes could be explained as a local effect of availability or as a real change in the size of a possible northern Tasmanian population, distinct from that of southern Victoria, although it is much more likely that there is only one population in Bass Strait (Blackburn and Gartner 1954).

The history of the fishery in eastern Tasmania over the same period has been quite different. In areas I, II, and III both the summer and autumn catches per unit effort vary a good deal from year to year, and in much the same way, the abundance in autumn being generally not much less than that in the preceding summer; in years when fish are markedly scarcer in autumn than in summer they are more plentiful than usual in spring (1948–49, 1952–53), which suggests an earlier arrival and departure of the main mass of the fish. Thus Figure 5 gives little information that was not given in Table 1, which indicated abundance and fishing success at a constant high level from 1947–48 to 1950–51, a slight drop in 1951–52, full recovery in 1952–53, and a disastrous fall in 1953–54. The data for area IV, further north on the east coast of Tasmania, tell almost the same story, although the years 1947–48 and 1950–51 were much better than the other good years. This last-mentioned fact, and verbal reports from eastern Tasmanian fishermen to the effect that barracouta were actually plentiful, but not biting, in the bad fishing season 1953–54, indicate the probable importance of availability effects upon fishing success in this region; but effects of real abundance (whole population size) might also be very significant.

The findings of this Section may be summarized as follows:

(1) On the south coast of Victoria the mean annual catch per unit effort of barracouta declined and then recovered over the period 1948–49 to 1953–54, the low point being 1950–51. It did so because catch per unit effort in the autumn quarter of the year, and to a less marked extent in the summer quarter, fluctuated from year to year in that way. These fluctuations were mainly effects of availability, not population size.

(2) On the north coast of Tasmania the mean annual catch per unit effort declined throughout over the same period, reflecting a decline in the autumn quarter in which effects of availability probably played the main part.

(3) On the east coast of Tasmania the mean annual catch per unit effort remained fairly stable over the same period until it fell in 1953–54, reflecting a similar trend in summer and autumn. There is evidence that availability effects contributed to this trend, but the possibility of major effects of population size cannot be denied.

V. Discussion

It was shown in Section IV that an effect of availability, i.e. some feature of the distribution or behaviour of the barracouta populations, plays, in summer and especially in autumn, the major part in determining the success or failure of the year's fishing on the south coast of Victoria; and probably so on the north coast of Tasmania, and possibly so on the east coast of Tasmania.

What do these barracouta populations do in summer and autumn? As stated in Section II of this paper, and by Blackburn and Gartner (1954), the gross features of their behaviour in summer are spawning (which some, however, have already completed in spring), feeding, and migration; and in autumn only feeding and migration. Spawning is therefore unlikely to be the key to the problem. About migration little can be said, except that it seems to be a leisurely process—the return migration of the Bass Strait population through the Strait is generally first evident in the catch records in March and is not over until the end of June (Blackburn and Gartner 1954)—in the course of which the fish search for food. At this time they may deviate considerably from their general easterly course, presumably for food, as shown by the fact that they are nearly always more plentiful in autumn in areas X and XI than in area XII (Blackburn and Gartner 1954); that is to say, they do not go northwards into this bight merely to follow the coast east, because many of them follow it only to the head and then take another route. So the search for food—not always plentiful, and seldom so in March and April (Figs. 2 and 3)—probably largely determines the distribution of the barracouta in the immediate coastal waters in summer and especially in autumn, particularly in the southern Victorian bight.

It was shown in Section II that *Nyctiphanes australis* is the only item of the diet of barracouta which is freely available from December to April on the south coast of Victoria and from February to May on the east coast of Tasmania, and that a similar situation probably exists in the south, east, and west of Bass Strait at about the same times of year; and that *Nyctiphanes* is utilizable by barracouta only when it occurs in fairly dense concentrations.

These observations suggest that the availability of fish in a certain area in the summer and autumn of a particular year depends upon the availability of *Nyctiphanes* there. If *Nyctiphanes* is plentiful and well concentrated in the coastal fishing areas barracouta will be there, otherwise they will go elsewhere; there are vast unfished areas to which they could go.

The only data available for testing this hypothesis are those of Section III (year-by-year percentages of coastal barracouta feeding on *Nyctiphanes*) which may be compared with the data of Section IV on annual fluctuations in availability of coastal fish. They are available only for areas X, XI, and XII (Sections III(*a*)) and areas I, II, and III (Section III(*b*)).

In the former region as a whole, the amount of feeding on *Nyctiphanes* in summer and autumn in the period 1948–49 through 1953–54 declined and then rose, 1950–51 and 1951–52 being the years when this food was most sparse (Fig. 4). The abundance of barracouta in this region as a whole shows a somewhat similar trend (Fig. 5) but with only one poor year (1950–51) instead of two. However, it was shown by Blackburn and Gartner (1954, Figs. 12–14) that the recovery in availability in 1951–52 was not uniform for the whole bight; it was complete only in area X, incomplete in area XI, and not evident at all in area XII. It was stated in Section III(*a*) of this paper that hardly any of the stomach material of 1951–52 was obtained from area X. So the two sets of data for the whole bight for 1951–52 could not be expected to agree as well as they do in other years. For want of sufficient feeding data it is not practicable to dissect all the information of Figure 4 according to the separate areas X, XI, and XII. If area XI and area XII data are grouped 1949–50 appears to be a good year, 1950–51 a bad one, and 1951–52 slightly better than the preceding, both as regards catch per boat-month and percentage of stomachs containing *Nyctiphanes*, but even so there is no significant correlation; this could hardly be expected with any of the data of Figure 4, which are useful only for the recognition of gross annual trends.

There is thus reasonable support for the abovementioned hypothesis as far as this bight is concerned, if it may be assumed that *Nyctiphanes* was more abundant in area X than elsewhere in the autumn of 1952. This could easily have happened, as shown by planktological data obtained in the autumn of 1954, which are mentioned below.

For areas I, II, and III combined, the percentage of autumn stomachs containing *Nyctiphanes* fell from 1949–50 through 1952–53, and so did the catch per boat-month of barracouta, although again the correlation is not significant; the year 1948–49 is ignored, for reasons given in Section III(*b*). For the summer quarter the only comparison that can be made is of 1951–52 against 1952–53. The percentage of stomachs containing *Nyctiphanes* showed the same fall as in the corresponding autumns, but the catch per boat-month rose in 1952–53; however, there was a great increase in 1952–53 in the percentage of stomachs with non-euphausiid food, which is often considerable in summer (Fig. 3), and no correlation between availability of fish and availability of *Nyctiphanes* could be expected under such circumstances.

No stomachs were collected in 1953–54, the year of minimum availability of barracouta to the fishermen. However, the same fishermen who reported that barracouta were abundant, but not biting, referred to the presence in the fishing areas of large concentrations of *Nyctiphanes*. A research vessel also encountered such concentrations during very brief visits to the region in December and February. The fishermen believed that the fish would not bite because they were surfeited with food, an opinion which is heard from time to time under similar circumstances in most Australian barracouta fishing ports. Such an availability effect could exist and warrants proper investigation, but for the present it remains merely an interesting possibility. Should it be real there would be an upper as well as a lower limit to the range of availability of *Nyctiphanes* within which positive correlation with availability of barracouta to line fishermen could be expected.

It was noted in Figure 5 that availability of barracouta declined in 1953–54 in the Victorian area IX, although not in areas X, XI, and XII. This could be explained in relation to availability of *Nyctiphanes*, as a fisherman's report from the area referred to a great shortage of "brit" for most of that year. A research vessel on a brief visit in March 1954 did not find any *Nyctiphanes* although she found it elsewhere and had seen a great deal of it in area IX in March and May of the previous year.

The shortage of *Nyctiphanes* in northern Tasmanian waters in April 1951 was remarked on in Section II(*b*); only 5 per cent. of stomachs contained this food although 69 per cent. were empty. Barracouta were very scarce.

The comparative scarcity of barracouta in areas X, XI, and XII in the spring of 1950 could reflect the shortage of anchovy which apparently occurred then (Fig. 4, cf. Fig. 2).

Two questions which remain are: where may *Nyctiphanes* be found when they are not plentiful in Bass Strait coastal waters? and do barracouta also go there? The answer to the first question is that *Nyctiphanes* are frequently plentiful in the most offshore parts of Bass Strait. To the second question, the answer is that the barracouta is quite capable of going anywhere in Bass Strait (Blackburn and Gartner 1954, tagging results) but that no record exists of its capture beyond 30 miles offshore; there has, however, been very little fishing more than 20 miles from the coasts (Blackburn and Gartner 1954).

Mention may be made of a synoptic oceanographic survey of Bass Strait made in March 1954. The results as regards distribution of *Nyctiphanes australis* will be published in more detail elsewhere, but the main feature was maximum density of this species in a band crossing Bass Strait in area VI from the Tamar River mouth on the north coast of Tasmania (where little barracouta fishing is done) to area X on the Victorian coast, which was the only part of Bass Strait where fishing was good in that month. Such a distribution in the autumn of 1952 could have accounted for the improvement of the fishery which occurred in only the western part of the bight at that time.

In any event it is clear that the staple food of the barracouta in autumn can be abundant and widespread in other parts of Bass Strait when it is scarce on the coasts, and that the fish could go there instead of remaining on the coasts. It remains to be shown, by sustained slow-speed fishing experiments in offshore areas containing *Nyctiphanes*, that fish actually do this. It is quite possible, of course, that the supply of *Nyctiphanes* could sometimes fail altogether in all parts of Bass Strait.

The hypothesis that annual fluctuations in the success of the barracouta fisheries of Bass Strait depend mainly upon corresponding fluctuations in the availability of *Nyctiphanes australis* ("brit") in the coastal waters in summer and autumn, is thus an attractive one, warranting further testing. It may also have some application to eastern Tasmania.

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THE RESPIRATORY METABOLISM OF *DENDROSTOMUM CYMODOCEAE* EDMONDS (SIPUNCULOIDEA)

By S. J. Edmonds*

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Summary

The consumption of oxygen of *Dendrostomum cymodoceae* at 22°C in aerated sea-water varied from 4·5–5·5 μl/g (wet weight)/hr for adults to 20–31 μl/g/hr for juveniles. The production of carbon dioxide was 13–17 μl/g/hr (juveniles) and the R.Q. varied from 0·55 to 0·67 (juveniles). The rate of consumption of oxygen decreased as the tension of the dissolved oxygen decreased. The oxygen combined with the pigment of the blood was 2·1 vols. of oxygen per 100 vols. of blood and the ratio of blood volume (ml) to total weight (g) of the animal was 0·47. *D. cymodoceae* was able to live under anaerobic conditions in sea-water for as long as 5 days and in paraffin oil for 4 days. The haemerythrin in the blood of animals kept under oil was found to be reduced after about 6 hr. Lactic acid was identified as one of the end-products of anaerobiosis. The concentration of lactic acid in the blood of animals living under anaerobic conditions increased after 60 hr from 7–12 to 45–61 μg/ml of blood. The ability to revert to anaerobiosis may have survival value for the species.

I. Introduction

This paper deals with: (1) the consumption of oxygen, the production of carbon dioxide, and the respiratory quotient under aerobic conditions of *Dendrostomum cymodoceae* Edmonds, 1956; (2) the ability of the animal to live under anaerobic conditions, and the nature of the end-products of anaerobic metabolism.

There is evidence to show that some invertebrates, normally aerobic, can live for a number of days under anaerobic conditions. Peebles and Fox (1933) kept *Dendrostomum zostericola* alive for 7 days in "Nujol" oil from which the air had been removed. Hecht (1932) kept *Arenicola marina* under conditions of anaerobiosis for several days and *Nereis* sp. for more than 8 days, von Brand (1927) *Owenia fusiformis* for more than 21 days, and Alsterberg (1922) *Lumbriculus* sp. for more than 10 days and *Glossiphonia* for 5 days. Other records are listed and critically examined by von Brand (1945). Experiments described in the present paper show that *D. cymodoceae* can be added to the list.

II. Material

D. cymodoceae occurs in South Australia amongst the thick and tangled roots of the marine angiosperm, *Cymodocea antarctica* Endlicher, just below the level of the lower spring tides. Juveniles of the species can move to some extent amongst the sand and debris between the roots. Adults, however, are always found firmly wedged into a flask-shaped cavity and are sedentary.

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Animals after being collected and before use in any experiment were placed in a well-aerated aquarium for 4 days. In this time the gut became empty. All experiments, therefore, were performed with fasting animals.

III. Experiments and Methods

(*a*) The consumption of oxygen and the production of carbon dioxide by juvenile specimens at 22°C was determined by the direct method of Warburg, using cups of 15 ml capacity. Three or four animals, each weighing 0·6–0·8 g, were used in each determination.

(*b*) The consumption of oxygen of adults at 22°C was determined by the standard Winkler method. Ten to twelve animals, each weighing 8–10 g, were placed in 600 ml of well-aerated sea-water, which was sealed with 2–3 in. paraffin oil (B.P.) during the experiment.

(*c*) Two experiments somewhat similar to those described by Peebles and Fox (1933) with *D. zostericola* were conducted with *D. cymodoceae*:

(i) Sea-water was placed in a number of florence flasks and boiled to remove dissolved gases. The water was allowed to cool while a stream of nitrogen freed from oxygen by passing it over heated copper turnings at 400°C was bubbled through it. An adult sipunculid was placed in each flask and more nitrogen bubbled through the solution for about 30 min. The flasks were then stoppered tightly to prevent the re-entry of air.

(ii) Oxygen-free nitrogen was bubbled for 6 hr through a florence flask filled with liquid paraffin. An adult animal was placed in each flask, nitrogen again bubbled through the liquid for 30 min, and the flasks tightly stoppered.

In both experiments (i) and (ii) rubber stoppers were used and no gas was left at the top of the flasks. The stoppers after fixing were smeared with vaseline and at the end of the experiments had not been disturbed. No checks were made to see if the stoppering technique prevented the entry of air. Because subsequent experiments showed that the combined oxygen of the blood of animals kept in oil under such conditions was reduced to a very low level, it was assumed that the stoppering technique was effective.

(*d*) To examine the development of an "oxygen debt", the oxygen consumption of 10 animals was determined over a period of 6 hr by the Winkler method. The animals were then removed from the sea-water and quickly transferred to a fresh supply of aerated water. The consumption of oxygen of the same animals was redetermined during a period of 6 hr.

(*e*) The oxygen combined with the blood pigment of *D. cymodoceae* was determined by the action of potassium ferricyanide on the blood in a modified Warburg respirometer flask according to the method of Maegraith, Jones, and Sculthorpe (1950). Haemerythrin, like haemoglobin, liberates dissolved oxygen when treated with potassium ferricyanide (Florkin 1933*b*, pp. 255–64). Adult animals were left overnight in an aerated aquarium. 2·0 ml of oxygenated blood was withdrawn from the animal and introduced into the flask below a layer of borate buffer of pH 10. After equilibration potassium ferricyanide was tipped in from a side-arm and the volume of oxygen expelled measured in a manometer.

By using the same method the combined oxygen of the blood of animals kept under anaerobic conditions for different periods of time was determined. Five flasks were almost filled with paraffin oil, through which oxygen-free nitrogen was bubbled for 6 hr. An adult sipunculid was placed in each flask and nitrogen again bubbled through the oil. The flasks were then tightly stoppered. After intervals of 6, 12, 18, 24, and 48 hr the stopper was removed from a flask and the animal cut under oil. The blood collected at the bottom of the flask. 2·0 ml was then withdrawn in a pipette, so that a layer of oil floated on top of the blood, and transferred to the modified respirometer flask. The volume of oxygen combined with the pigment in the blood was then determined as described above.

(*f*) The relation between the volume of blood contained by an animal and its weight was determined by wiping 10 larger animals, weighing them, and bleeding them. The fluid was collected and measured in graduated cylinders.

(*g*) In order to determine, if possible, the end-products of anaerobiosis the blood of animals of approximately the same weight (9–10 g) kept under (i) aerobic, and (ii) anaerobic conditions in oil for 2 or 3 days was tested for organic acids by paper chromatography. The method used was that of Ladd and Nossal (1954). After remaining in oil for 3 days the animals were withdrawn and carefully washed. They were then punctured and the blood quickly transferred to a mortar and ground with "Celite" and 1 ml 0·1N sulphuric acid. The mixture was placed in a Soxhlet thimble and the organic acids extracted for 12 hr with ether in a Soxhlet flask. The acids were obtained after evaporation of the extract as ammonium salts. These were then run on Whatman No. 1 filter paper in a solvent of *n*-butyl and *iso*butyl alcohols and formic acid.

(*h*) The amount of lactic acid present in the blood of animals kept in oil under anaerobic conditions for different periods of time was determined by the method of Barker and Summerson (1941). Four flasks were filled with paraffin oil through which oxygen-free nitrogen was bubbled for 6 hr. Into each was placed a sipunculid weighing 10–12 g. More nitrogen was passed through the oil and the flask stoppered. The same stoppering technique was used as described under (*c*). After 12, 24, 48, and 60 hr, a flask was opened and the animal removed and bled. Estimations were made on 1 ml of blood from which proteins were removed by trichloroacetic acid.

IV. Results

(*a*) *Consumption of Oxygen and Production of Carbon Dioxide*

(i) The consumption of oxygen by juveniles at 22°C was found from five determinations (Warburg) to be $26 \pm 3{\cdot}6$ μl/g (wet weight) hr.

(ii) The consumption of oxygen by adults at 22°C during six 1-hr intervals (standard Winkler estimations) is shown for three experiments in Figure 1. Allowance was made for the oxygen dissolved in the reagents.

(iii) The production of carbon dioxide by juveniles at 22°C from five determinations was found to be $16 \pm 1{\cdot}6$ μl/g (wet weight)/hr.

(b) *Respiratory Quotient*

The R.Q. of fasting juveniles was derived from Q_{O_2} and Q_{CO_2} values as shown in Table 1. The average value was 0·60.

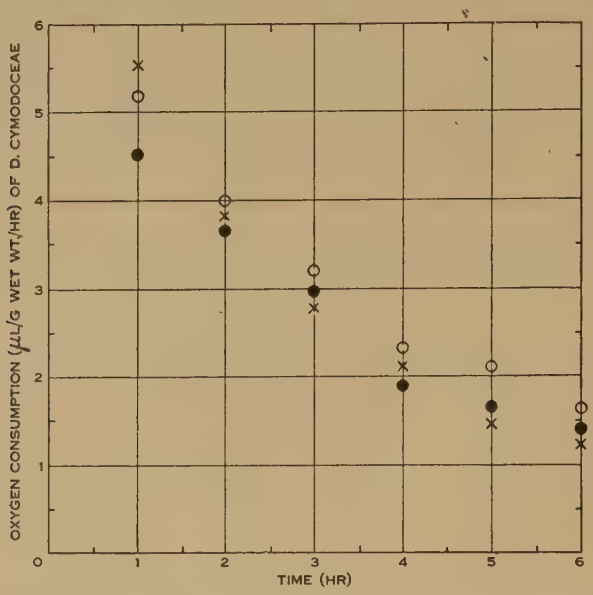

Fig. 1.—Consumption of oxygen of *D. cymodoceae* (results of three experiments).

(c) *Ability to Live under Anaerobic Conditions*

(i) Of 10 animals placed in sea-water under anaerobic conditions all responded to touch after 2 days, 8 after 3 days, 6 after 4 days, 1 after 5 days, and none after 6.

(ii) Of 10 animals placed in oil all responded to touch after 2 days, 5 after 3 days, 1 after 4 days, and none after 5.

TABLE 1

R.Q. OF FASTING JUVENILE SPECIMENS

Q_{O_2}	Q_{CO_2}	R.Q.
31	17	0·55
20	13	0·65
28	17	0·61
27	15	0·56
26	17	0·65

While kept anaerobically in sea-water and oil all the animals from time to time extended their introverts, the normal behaviour of living specimens. Animals kept anaerobically in sea-water for 4 days or in oil for 2 days usually recovered when placed in aerated sea-water.

These results show that *D. cymodoceae* was able to live as long as 5 days under conditions of anaerobiosis.

TABLE 2

THE VOLUME OF OXYGEN COMBINED WITH THE PIGMENT AND THE CONDITION OF THE BLOOD OF D. CYMODOCEAE DURING ANAEROBIOSIS

Time (hr)	Vol. of Oxygen Combined with 100 Vols. of Blood	Colour of Blood	Condition of Blood
0	1·9–2·5	Red	Oxygenated
6	0·3–0·4	Almost straw-coloured	Almost completely deoxygenated
12	0–0·2	Straw	Deoxygenated
18	0–0·1	Straw	Deoxygenated
24	0–0·2	Straw	Deoxygenated
48	0–0·1	Straw	Deoxygenated

(*d*) *Oxygen "Debt"*

In one experiment the total oxygen consumption of 100 g of animals after 6 hr was 2·04 ml. The total oxygen consumption of the same animals when replaced in a fresh supply of aerated sea-water was 2·28 ml after 6 hr. Therefore an oxygen "debt" of 2·4 μl/g was built up during this time. In a second experiment an oxygen debt of 2·8 μl/g was recorded after 6 hr.

TABLE 3

RELATION BETWEEN BLOOD VOLUME AND TOTAL WEIGHT OF D. CYMODOCEAE

Volume of Blood (ml)	Weight of Animal (g)	Ratio of Blood Vol. to Total Wt.
5·4	12·4	0·44
4·2	8·6	0·49
3·3	7·6	0·43
6·0	12·9	0·47
4·6	9·4	0·49
13·0	26·5	0·49
5·1	11·0	0·46
4·0	8·7	0·46
4·6	9·9	0·46
6·9	14·8	0·47

(*e*) *Combined Oxygen of the Blood*

(i) The results of 10 determinations showed that 100 vols. of blood at 22°C contained $2{\cdot}1 \pm 0{\cdot}2$ vols. of oxygen combined with the haemerythrin.

(ii) The volume of oxygen combined with the pigment in 100 vols. of blood of animals kept under anaerobic conditions for different periods of time is shown in Table 2.

(*f*) *Relation between Blood Volume and Weight*

The relation between the volume of blood contained by an animal and its weight is shown in Table 3.

The average value was 0·47. This corresponds with the value of 0·50 for *Sipunculus nudus* obtained by Florkin (1933*b*).

(*g*) *End-products of Anaerobiosis*

On spraying the paper with bromocresol green, evidence of the presence of an acid with an R_F value of 0·74–0·79 appeared above the application spots for animals kept under anaerobic conditions but not at all or only very faintly for those kept under aerobic conditions. The acid corresponded to lactic acid, whose R_F value was

TABLE 4

CONCENTRATION OF LACTIC ACID IN THE BLOOD OF SPECIMENS OF D. CYMODOCEAE DURING ANAEROBIOSIS

The figures in brackets give the weight of the animal in grams in each case

Time (hr)	Lactic Acid in Blood (μg/ml)			Average of 3 Determinations
	(i)	(ii)	(iii)	
0	7 (9·2)	12 (8·3)	11 (9·6)	10
12	10 (8·9)	19 (9·0)	25 (8·1)	18
24	22 (9·3)	33 (8·6)	29 (9·8)	28
48	39 (9·4)	35 (8·3)	46 (8·4)	40
60	45 (8·7)	49 (9·8)	61 (9·1)	52

shown by a control experiment to be 0·75. Traces of an unidentified acid with an R_F value of 0·44 were usually present with animals kept under oil. The possibility that this acid was a lower fatty acid was investigated by the paper chromatographic method of Reid and Lederer (1951). No spots, however, appeared on the paper. Tests for pyruvic acid were also negative.

(*h*) *Rate of Production of Lactic Acid*

Although all the lactic acid which forms during anaerobiosis does not necessarily appear in the blood it seems reasonable to assume that for animals of approximately the same weight the amount of lactic acid per millilitre of blood is a measure of its production. Table 4 shows lactic acid present in blood (μg/ml) after different intervals of time. Each determination was made on a different animal.

V. DISCUSSION

(*a*) The rate of consumption of oxygen in the adults, although low, was of the same order as the corresponding values for a number of other invertebrates. The comparative details set out in Table 5 (with the exception of those for *D. cymodoceae*) were selected from information gathered by Heilbrunn (1947, pp. 258–9).

(*b*) The difference between the oxygen consumption of the juveniles and the adults depended on the surface area of the specimens used. The ratio of the surface areas of specimens weighing 8–10 g and 0·6–0·8 g respectively was about $\left(\frac{9}{0{\cdot}7}\right)^{\frac{2}{3}}$, or 5, and the rate of consumption of oxygen of the juveniles was about 4–5 times that of the adults.

TABLE 5

OXYGEN CONSUMPTION OF A NUMBER OF INVERTEBRATES

Animal	Temperature (°C)	Oxygen Consumed (μl/g wet wt./hr)
SIPUNCULOIDEA		
Dendrostomum cymodoceae	22	4·5–5·5 (adults) 20–31 (juveniles)
ANNELIDA		
Arenicola sp.	10–12	31
Nereis virens	15	26
Chaetopterus sp.	15	8
MOLLUSCA		
Anodonta sp.	—	2
Mytilus sp.	22	55
Pecten sp.	—	9
Ostrea sp.	—	15
ECHINODERMATA		
Holothuria stellata	24–25	4
Holothuria impatiens	24–25	17
Strongylocentrus lividus	24–25	4–27

(*c*) The results of the experiments conducted with the adult specimens showed that there was a decrease in the consumption of oxygen as the experiment proceeded or as the oxygen tension fell. A decrease in the rate of consumption of oxygen with decrease in oxygen tension has been shown for *Nereis*, *Homarus*, *Limulus*, and *Callinectes* (Amberson, Mayerson, and Scott 1925; Amberson 1928), *Caudina chilensis* (Nomura 1926), *Patiria miniata* (Hyman 1929), and *Sipunculus nudus* (Henze 1910). The metabolism of *Dendrostomum* at low oxygen levels is dealt with in another part of this discussion.

(*d*) The R.Q. of the juvenile specimens was lower than that normally obtained for other marine animals. No satisfactory explanation is suggested.

(*e*) The value for the combined oxygen of *D. cymodoceae*, 2·1 vols. of oxygen per 100 vols. of blood, agrees fairly closely with the value of 1·6 vols. of oxygen per 100 vols. of blood, obtained for the oxygen capacity of the blood of *Sipunculus nudus* by Florkin (1933*a*, 1933*b*) using the method of Van Slyke. Florkin's conclusion that the oxygen capacity of *Sipunculus* is low compared with that of a number of other invertebrates applies therefore to *Dendrostomum*. The oxygen capacity of the blood

of the echiurid *Urechis caupo* (in which the pigment is haemoglobin) is 2·16–6·7 vols./100 vols. (Redfield and Florkin 1931), of the annelid *Arenicola* (haemoglobin) 5·7–8·2 vols./100 vols. (Fox 1926), and of the molluscs *Loligo* (haemocyanin) 3·8–4·5 vols./100 vols. (Redfield, Coolidge, and Hurd 1926) and *Octopus* (haemocyanin) 3·9–5·0 vols./100 vols. (Winterstein 1909; Wolvekamp 1932).

(*f*) The volume of oxygen combined with the haemerythrin in an animal weighing 10 g is $10 \times 0{\cdot}47 \times 21$ or about 100 μl. This, if consumed at the rate of 4–5 μl/g/hr, would permit the animal to live 2–3 hr in water lacking dissolved oxygen. The consumption of oxygen, however, decreased as the tension of the dissolved oxygen decreased, so that the value of 2–3 hr is too small. A value of 6 hr is probably nearer the mark, because the pigment of animals kept under oil was almost completely deoxygenated after that time. As it occurs amongst *Cymodocea antarctica*, the upper level of which is about the level of the lower lows of the spring tides, *D. cymodoceae* may find it necessary occasionally to draw upon the reserve of oxygen in its blood. This period of time would normally be no longer than 3–4 hr. Redfield and Florkin (1931) found that the oxygen stored in the blood of *Urechis caupo* was sufficient to meet the normal requirements of the animal for about 1 hr, and Borden (1931) that the oxygen dissolved in the fully saturated blood of *Arenicola* was sufficient to last over a period of 71 min.

(*g*) The pigment of specimens kept under oil was deoxygenated probably after 6 and certainly after 12 hr, so that little or no oxygen was available for aerobic processes. In spite of this the animals continued to live for 3 or 4 days. The conclusion is that during this time *D. cymodoceae* was in a condition of anaerobiosis and that as the quantity of lactic acid in the blood of the animal increased significantly this acid was one, and possibly the chief, end-product of anaerobiosis. No information can be given about the substrate used during anaerobiosis. It is known, however, that a considerable amount of glycogen occurs in *Sipunculus* and a number of sessile polychaets (von Brand 1927, p. 686; von Brand 1945).

Of what importance to the animal is its ability to survive under anaerobic conditions? Although its trunk is usually found amongst a tangled mass of roots containing sand and debris, a region of low oxygen concentration, it is unlikely that *D. cymodoceae* normally has to endure low levels of oxygen tension for long periods of time provided that it can extend its introvert into aerated water. It is possible, however, that during rough weather sand and debris may be deposited to depths of 4–5 in. or more on top of patches of *Cymodoceae*. These temporary layers of sand and pebbles may prevent aerated sea-water from reaching the animal. At such times the ability to revert to anaerobiosis may ensure survival. Perhaps, too, it may be of importance to juveniles in unfavourable environments, as their consumption of oxygen is considerably higher than that of adults.

VI. Acknowledgments

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THE ASCIDIANS OF AUSTRALIA

II. APLOUSOBRANCHIATA LAHILLE: CLAVELINIDAE FORBES & HANLY AND POLYCLINIDAE VERRILL

By Patricia Kott*

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Summary

An account is given of 39 species of Australian ascidians of the families Clavelinidae and Polyclinidae, of which 14 are new. The larvae of certain species are considered in relation to specific and phylogenetic patterns within the genera and families. The geographical distribution of species is discussed.

I. Introduction

In part I of this series (Kott 1952*a*), Australian ascidians of the suborders Stolidobranchiata Lahille and Phlebobranchiata Lahille were dealt with. The present work concerns all subfamilies of the Clavelinidae; and in the Polyclinidae all genera of the subfamily Euherdmaninae and the aberrant genus *Sidneioides*, subfamily Polyclininae. Fourteen new species are recorded and described in the genera *Eudistoma*, *Polycitor*, *Clavelina*, *Podoclavella*, *Distaplia*, *Pseudodistoma*, *Ritterella*, and *Euherdmania*; and the geographical distribution of species is discussed. Distribution of these species around Australia agrees generally with established geographical regions (Kott 1952*a*). The ascidian fauna of the Dampierian and Solanderian regions often includes East Indies, Malayan, and even Red Sea species; East African and Indian Ocean species occur particularly in the Dampierian region.

The present work is based on the same collections as those for part I of the series, including the collection in the Australian Museum, Sydney, where Herdman's (1899) type specimens are located. These collections were augmented by the author during 1948–1955. All type specimens for new species described herein are lodged in the Australian Museum, Sydney.

Keys are given for each genus. Since certain species have a distribution extending beyond Australia into the Indo-Malayan, Pacific, and sub-Antarctic areas, species recorded from these latter areas are included in the keys. The known distribution of each species is given as an aid to identification, and so that distinctions between related species in adjacent areas are apparent. Also, as the literature is particularly diffuse, a recent reference is given, in parenthesis, for those species which are not otherwise discussed. Species marked with an asterisk in the keys are those discussed herein. Australian records only accompany species descriptions. These are given in order from north-west, south to north-east.

Conventions used in descriptions are those generally used by workers in the group, except that here it has been found necessary to standardize the terms describing various divisions of the intestine. Thus, the duodenum is the narrowed portion of the

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intestine immediately following the stomach, and occasionally terminated distally by a posterior stomach enlargement; the mid intestine is the area between the posterior stomach and the rectum, or between the duodenum and the rectum when the posterior stomach is absent.

In determining the number of stigmata in each row of the branchial sac, a row of stigmata on one side only is considered to constitute a "row of stigmata".

Full descriptions of larvae are given, except in those few species in which embryos were not present in the brood pouch of the adult. Where larvae were present they have been used to assist in the characterization of the species.

The general outline of the classification used is that given by Huus (1937) with modifications in the Clavelinidae after Berrill (1950).

II. Classification

Suborder **APLOUSOBRANCHIATA** Lahille

Colonial; body divided into thorax and abdomen; posterior abdomen may or may not be present. Branchial sac without internal longitudinal vessels or folds. Gut in the abdomen; gonads in abdomen or posterior abdomen.

Family **CLAVELINIDAE** Forbes & Hanly

Colonies of variable form but seldom flat. Zooids divided into thorax and abdomen; no obvious posterior abdomen. Gonads in loop of gut. Branchial sac with variable number of rows of stigmata.

Subfamily **POLYCITORINAE** Michaelsen

Siphons both 6-lobed. Zooids either opening independently or arranged in systems. Budding by abdominal constriction. Stolonic vessel with mesenchymatous septum weakly developed (Berrill 1936).

Subfamily **CLAVELININAE** Seeliger

Siphons independent, smooth-bordered. Buds formed as mesenchymal statoblasts accumulating at terminal branches of stolonic vessel.

Subfamily **HOLOZOINAE** Berrill

Zooids more or less in systems. Branchial siphon 6-lobed, atrial siphon with modified languet. Buds produced from epicardium in isolated tip of abdomen. Stolonic vessel present.

Family **POLYCLINIDAE** Verrill

Colonies mostly massive. Zooids divided into thorax, abdomen, and post-abdomen. Heart and gonads in post-abdomen. No stolonic vessel (Berrill 1936). Budding by abdominal strobilation.

Subfamily **EUHERDMANINAE** Seeliger

Atrial siphon 6-lobed, opening independently.

Subfamily **POLYCLININAE** Adams*

Atrial apertures usually with languet, never 6-lobed, opening into common cloaca.

Family **DIDEMNIDAE** Giard*

Colony usually flat, investing. Test usually with spicules. Body divided into thorax and abdomen. Branchial sac with 3–4 rows of stigmata. Gonads in loop of gut; no oviduct. No stolonic vessel.

III. Family **CLAVELINIDAE**

Carlisle (1953) suggests a closer phylogenetic relationship between the Polycitorinae and Polyclinidae than between the former subfamily and other members of the Clavelinidae. He bases his argument, firstly, on the "spilling over" of the gonads and the heart from the abdomen into a post-abdominal extension in certain individuals of the Polycitorinae. This shows that the condition of the post-abdomen, the main morphological distinction between the Polycitorinae and the Polyclinidae, is only different in degree in the two groups. Secondly, he notes the similarity of the form and structure of gonads in the Polycitorinae and species of *Polyclinum,* the more primitive genus of the Polyclinidae.

After an examination of many species of all subfamilies of the Clavelinidae, however, it is apparent that similar arguments could be used to relate not only the Polycitorinae but also the Clavelininae and the Holozoinae to the Polyclinidae; and the morphology of the gonads in certain species of Holozoinae are particularly identifiable with the condition found in *Polyclinum.* Apparently there is a tendency throughout the Aplousobranchiata towards a "spilling over" of the gonads and heart into a posterior abdominal extension; although only in certain species of Holozoinae and in the Polyclinidae are the gonads completely removed from the alimentary canal and accommodated in a posterior abdomen. It is therefore not a primary characteristic in itself, although in company with other features it is useful in separating the major phylogenetic groups of this suborder.

The Polycitorinae and the Polyclinidae are both groups which bud by the primitive strobilation of the abdomen; while Holozoinae and Clavelininae have developed a more specialized means of budding (Berrill 1936, 1950). Associated with this is the hypertrophy of the stolonic vessel in the latter two subfamilies. This stolonic vessel is present in Polycitorinae but not hypertrophied. However, it is not present in Polyclinidae. In addition to and associated with a stolonic vessel as a primary character uniting the subfamilies of the Clavelinidae there is a tendency to a shortening of the short limb of the primitive V-shaped heart, present in *Ciona* and the Diazonidae and unmodified in the Polyclinidae. This shortening of the heart in the Clavelinidae culminates, in the Clavelininae, in a straight heart.

Apparently both the Clavelinidae and the Polyclinidae have been derived from some primitive *Ciona*-like ancestor, by dwarfing and a concurrent simplification of the branchial sac. In the former, however, this has been accompanied by the develop-

* Only the aberrant genus *Sidneioides* in the Polyclininae is dealt with here and Didemnidae are not discussed at all.

ment of a stolonic vessel, a shortening of the heart, and a tendency toward a specialized system of budding. In the latter, the dwarfing has been accompanied by a shortening of the gut and an extension of gonads and heart into the posterior abdomen.

Carlisle (1953) has also drawn attention to the similarity of larvae in Polyclinidae and Polycitorinae. He states that the main difference is the posterior extension of the lateral germ ridges in the former family. In the same work he has described the larva of *Polycitor crystallinus* Renier as typical of the subfamily Polycitorinae, with eight ampullae around the suckers, and has compared it to the larva of *Polycitor searli* Kott (1952*b*).

The larva of *P. searli* has a median vertical line of ampullae alternating with the suckers, and this has since been confirmed by the author. Median unpaired ampullae also occur in the larvae of *Eudistoma globosum*, sp. nov., *E. parvum* Sluiter, and *E. elongata* (Herdman). Therefore although many of the larvae of Polycitorinae species do have eight ampullae arranged in pairs, larvae with four median unpaired ampullae only also occur. In order to distinguish between the larvae of Polycitorinae and Polyclinidae, and to establish relationships between these and other subfamilies of the Clavelinidae, it is necessary to examine more closely the development of the larvae with paired rather than unpaired median ampullae. By an examination of embryos at different stages in certain species, it has been ascertained that the paired ampullae in Polycitorinae arise from the median projections between the suckers, and the earlier embryos of these species appear similar to the earlier embryo of *Eudistoma elongata* in the present collection (Fig. 10). These median projections divide down the median line and appear in the later embryo as paired ampullae. It is significant that all known larvae of the Polycitorinae with paired ampullae do not have median ampullae as well, while in most cases the median ampullae are retained in addition to the lateral ampullae in the Polyclinidae. Also, in support of the evidence that paired ampullae in Polycitorinae are derived from the median line, while those of Polyclinidae are derived from the lateral germinal ridge, is the fact that in Polyclinidae the tail is always curved around between the suckers and the right row of ampullae; while in the Polycitorinae the tail is always curved around outside all ampullae.

Therefore in addition to the posterior extension of the lateral germ ridge in Polyclinidae, Polycitorinae may also be distinguished by the fact that the lateral germ ridge is apparently not differentiated at all; and paired ampullae are analogous rather than homologous with the paired ampullae found in the Polyclinidae.

In other subfamilies of the Clavelinidae the primitive triradiate arrangement of the suckers is retained with one sucker to the right of the tail and two suckers to the left. As the embryo develops, the tail assumes a horizontal position around the trunk from left to right; thus forcing the right sucker ventrally and the two suckers on the left into a dorsal position, where they are found in the fully developed larva. Numbers of these species, particularly *Podoclavella meridionalis* (Fig. 24), develop an ampulla alongside each sucker. By a reduction in size of the larva it is possible that both the suckers and their accompanying ampullae might be forced into the

median vertical line to the left of the tail where they are found in the larvae of the Polycitorinae.

The larvae of Polycitorinae therefore support the morphological evidence from the adult that the subfamily is no more closely related to Polyclinidae than are either the Clavelininae or the Holozoinae; that it has primary characters in common with the latter two subfamilies; and that the three subfamilies of the Clavelinidae have evolved from a primitive ancestor in a similar direction, but different from the line of evolution found in the Polyclinidae. The Polycitorinae are possibly more primitive morphologically than either of the other groups, although their larva has been modified from the primitive form by a reduction in size.

For these reasons it is considered that by retaining the family Clavelinidae to comprise subfamilies Polycitorinae Michaelsen, Clavelininae Seeliger, and Holozoinae Berrill, less violence is done to the phylogenetic relationships of the group than would be done by following Carlisle's (1953) suggestion and separating Polycitorinae from the other subfamilies of the Clavelinidae.

Subfamily **POLYCITORINAE**

Genus CYSTODYTES Drasche

Four rows of stigmata; test with disk-shaped spicules.

Key to Species of Cystodytes

1. With stellate spicules ..... *C. tasmanensis* Kott
   Tasmania (Kott 1954)
   Without stellate spicules 2
2(1). Three rows of stigmata; 5–6 in a row ..... *C. rufus* Sluiter
   North Borneo (Sluiter 1909)
   Four rows of stigmata; more than 6 in a row 3
3(2). Spicules few and imperfect ..... *C. lobatus* (Ritter)
   California (Van Name 1945)
   Spicules many and perfect 4
4(3). Some spicules with notched borders 5
   No spicules with notched borders 6
5(4). Cone-shaped spicules ..... *C. rosaleus* Hartmeyer
   Seychelles, South Africa, Gulf of Guinea (Michaelsen 1919)
   Lens-shaped spicules ..... *C. morifer* Michaelsen
   South-west Africa, Madagascar (Michaelsen 1919)
6(4). Spicules completely enclose zooid; atrial siphon posterior ..... *C. variabilis* Sluiter
   East Indies (Sluiter 1909)
   Spicules form cup for zooids; atrial siphon not posterior 7
7(6). Largest spicules 100 μ ..... *C. semicataphractus* Sluiter
   East Indies (Sluiter 1909)
   Largest spicules greater than 200 μ ..... *C. dellachiaiae* (Della Valle)*
   Atlantic, Pacific, and Indian Oceans, Mediterranean

Cystodytes dellachiaiae (Della Valle)

Distoma dellechaijae Della Valle, 1877, p. 40.
Cystodytes dellachiaiae Kott, 1954, p. 154, for synonymy and literature.

Records.—Shark Bay, W.A. (Michaelsen 1930); Rottnest I., Garden I., and Albany, W.A.; Maria I., Tas. (Kott 1954).

* Indicates species referred to herein.

Discussion.—The specimens agree in all respects with those previously described. Larvae are present in the test of some specimens and are identical with those from Tasmania collected by the B.A.N.Z. Antarctic Research Expedition (Kott 1954).

Genus ARCHIDISTOMA Garstang

Three rows of stigmata; stomach smooth; thorax of zooids free from common test.

There is only one specimen of the genus *Archidistoma* Garstang in the present collection—*Archidistoma parva* (Sluiter). It seems probable (Berrill 1950; Kott 1952*b*) that there is no true distinction between this genus and *Eudistoma*. The latter generic name should therefore be dispensed with in favour of the prior term *Archidistoma*. However, *Eudistoma* has here been retained as the genus, in view of the large number of species concerned; and the one species of *Archidistoma* is included in the key to the genus *Eudistoma*.

Archidistoma parva (Sluiter)

Distoma parva Sluiter, 1900, p. 6.

Records.—Pulbah I., Lake Macquarie, N.S.W.

Colony.—Glassy, transparent, club-shaped, 5·0 mm high; basally test invested with sand. Zooids open separately to surface. Surface raised over anterior portion of zooids.

Zooid.—3·0 mm long; thorax one-third the length of whole body. Apertures on fairly long siphons; branchial siphon terminal, atrial siphon anterodorsal and larger than branchial siphon. Three rows of stigmata with about 8 stigmata in each row. Stomach round, smooth, and half way down abdomen.

Discussion.—This small species has a very wide distribution, extending from the East Indies to New South Wales. The very few records of its existence may be due to its small size. The size, distribution, and simple form of the colony and zooids suggest the possibility that rather than being a species these forms may represent the young colony of several distinctive adult species. However, this seems unlikely as gonads are present; and stigmata, even in the larval forms of other species, are usually more numerous than those found here in the adult.

Genus EUDISTOMA Caullery

Three rows of stigmata; stomach smooth; zooids completely enclosed in common test.

Key to Species of Eudistoma

1. Atrial siphon level with posterior row of stigmata 2
   Atrial siphon anterior to posterior row of stigmata 4

2(1). Atrial siphon posteriorly directed, opening in central common cloaca ..... *E. deerata* (Sluiter)
   Malaya, Torres Strait, Great Barrier Reef (Hastings 1931)
   Atrial siphon anteriorly directed, opening on surface of colony 3

3(2). Extensive prestigmatal zone ..... *E. ianthinus* (Sluiter)
   East Indies (Sluiter 1909)
   No extensive prestigmatal zone ..... *E. torosus* (Sluiter)
   East Indies (Sluiter 1909)

4(1). Oesophagus short; abdomen not longer than thorax 5
Oesophagus long; abdomen longer than thorax 6

5(4). Intestine not differentiated from rectum ..... *E. mjobergi* (Hartmeyer)
North-west Australia (Hartmeyer 1919)
Intestine differentiated from rectum ..... *E. cyanea* (Herdman)*
East Indies, Malaya, Aru I., north-west Australia, Rottnest I. (W.A.), New South Wales

6(4). More than 25 stigmata in each row 7
Less than 25 stigmata in each row 8

7(6). Thirty branchial tentacles ..... *E. multiperforata* (Sluiter)
Borneo (Sluiter 1909)
Ten branchial tentacles ..... *E. globosum*, sp. nov.*
Rottnest I., W.A.

8(6). No distinct posterior stomach 9
With a distinct posterior stomach 28

9(8). Alimentary canal winds 10
Alimentary canal runs straight 12

10(9). Five to six stigmata in each row ..... *E. scaber* (Sluiter)
East Indies (Sluiter 1909)
Eight to 12 stigmata in each row 11

11(10). Stomach sharply cut off from oesophagus ..... *E. glaucus* (Sluiter)
East Indies (Sluiter 1909)
Stomach not sharply cut off from oesophagus ..... *E. arenaceus* (Sluiter)
East Indies (Sluiter 1909)

12(9). Abdomen segmented ..... *E. segmentatus* (Sluiter)
East Indies (Sluiter 1909)
Abdomen not segmented 13

13(12). Abdomen usually longer than 4 times length of thorax 14
Abdomen never longer than 3 times length of thorax 21

14(13). Branchial and atrial siphons confluent at base ..... *E. mollis* (Sluiter)
East Indies (Sluiter 1909)
Branchial and atrial siphons not confluent at base 15

15(14). Colony pillar-like, with stalk 16
Colony cushion-like without stalk 19

16(15). Intestine with inner spiral folds 17
No inner spiral folds in intestine 18

17(16). No black pigment; 7 stigmata in each row ..... *E. rhodopyge* (Sluiter)
East and South Africa (Michaelsen 1921)
With black pigment; 16 stigmata in each row ..... *E. kauderni* Michaelsen
Madagascar (Michaelsen 1921)

18(16). Twelve tentacles ..... *E. gilboviridis* (Sluiter)
East Indies (Sluiter 1909)
Thirty-two tentacles ..... *E. regularis* (Sluiter)
East Indies (Sluiter 1909)

19(15). Dome-shaped stomach; 7–9 stigmata ..... *E. circumvallatum* (Sluiter)
d'Urville I., N.Z. (Brewin 1946)
Stomach not dome-shaped; more than 9 stigmata 20

20(19). Cylindrical stomach; more than 9 longitudinal muscles ..... *E. arenosum*, sp. nov.*
Rottnest I., W.A.
Oval stomach; not more than 9 longitudinal muscles ..... *E. modestum* (Sluiter)
South-east Africa (Michaelsen 1921)

21(13). Stomach in pole of gut loop, barely enlarged ..... *E. laysani* (Sluiter)
East Indies (Sluiter 1909)
Stomach not in pole of gut loop; obviously enlarged 22

22(21). Stigmata of anterior row reduced in length dorsally 23
Stigmata of anterior row not reduced in length dorsally 24
23(22). Stigmata of posterior row reduced dorsally ..... *E. miniaceus* (Sluiter)
East Indies (Sluiter 1909)
Stigmata of posterior row not reduced dorsally ..... *E. caeruleus* (Sluiter)
South-east Africa (Michaelsen 1921)
24(22). Massive siphonal musculature ..... *E. renieri* Hartmeyer*
South-west Africa; Rottnest I., W.A.
Siphonal musculature not massive 25
25(24). Colony short, stalked; 5–6 stigmata in each row ..... *A. parva* (Sluiter)*
East Indies, New South Wales
Colony not short nor stalked 26
26(25). More than 12 stigmata in each row ..... *E. illotus* (Sluiter)
South Africa (Millar 1955)
Less than 12 stigmata in each row 27
27(26). With transparent heads ..... *E. loricatus* (Sluiter)
East Indies, Timor (Sluiter 1909)
Without transparent heads ..... *E. discolor* (Sluiter)
East Indies (Sluiter 1909)
28(8). Muscles in a continuous sheet on either side of body 29
Muscles not in continuous sheet on either side of body 30
29(28). Colonies thick and massive ..... *E. psammion* Ritter & Forsyth
California (Van Name 1945)
Colonies flat and encrusting ..... *E. diaphanes* Ritter & Forsyth
California (Van Name 1945)
30(28). With long atrial siphons; strong circular siphonal muscles 31
Atrial siphons short; no strong circular siphonal muscles 34
31(30). Siphonal sphincters present, not continuous around siphon 32
Circular siphonal muscles not concentrated into sphincter; continuous around siphon 33
32(31). More than 25 stigmata in each row ..... *E. angolanum* Michaelsen*
West Africa, north-west and south-west Australia
Not more than 25 stigmata in each row ..... *E. snakabri* Tokioka
Japan (Tokioka 1954*a*)
33(31). Proximal part of rectum forms S bend; 8–9 longitudinal muscle bands on thorax
..... *E. pyriforme* (Herdman)*
Japan, South Australia, Great Barrier Reef
Proximal part of rectum forms spiral twist; 4–6 longitudinal muscle bands on thorax
..... *E. ovatum* (Herdman)
Red Sea, South Africa, Torres Strait, north-west Australia (Hastings 1931)
34(30). Testes in a long coiled caecum ..... *E. amplus* (Sluiter)
Japan, East Indies, Malaya (Tokioka 1950)
Testes not in a long coiled caecum 35
35(34). Colony investing ..... *E. fantasiana*, sp. nov.*
Reevesby I., S.A.
Colony not investing 36
36(35). Thorax half length of abdomen ..... *E. tokarae* Tokioka
Japan (Tokioka 1954*a*)
Thorax less than half length of abdomen 37
37(36). Stigmata of anterior row extend anteriorly along dorsal median line ..*E. rubra* Tokioka
Japan (Tokioka 1954*a*)
Stigmata of anterior row do not extend along dorsal median line 38
38(37). Pillar-shaped colony; zooids open onto upper surface ..... *E. parvum* Oka*
Japan, New South Wales
Club-shaped colony; zooids open around head ..... *E. elongata* (Herdman)*
New South Wales, Queensland

Eudistoma cyanea (Herdman)

Colella cyanea Herdman, 1899, p. 70.
Sigillina caerulea Hartmeyer, 1919, p. 113, for literature and synonymy.

Records.—Cape Jaubert, W.A. (Hartmeyer 1919); Triggs and Rottnest Is., W.A.; Port Jackson, N.S.W. (Herdman 1899).

Colony.—A cylindrical head on a long stalk the same length as the head. Total length of largest colony 10 cm. Test soft, semi-transparent, and blue when alive. Zooids arranged in vertical rows along length of head, at right angles to surface. About 20 zooids in each row and about 14 rows around head.

Zooid.—5 mm long with thorax and abdomen of equal length. Apertures both 6-lobed on short siphons. Fourteen fine longitudinal muscle bands on thorax. Branchial sac wide, with 3 rows of 30 elongate stigmata. An extensive portion of the posterior part of branchial sac without stigmata. Sixteen branchial tentacles. Oesophagus short, stomach round and smooth; intestine clearly differentiated from rectum, forming short loop. Rectum crosses over oesophagus. Gonads present as usual in loop of gut. A long fine vessel from end of abdomen extends down into stalk of colony.

Discussion.—The present specimens are smaller than those described by Sluiter from the East Indies, but larger than Hartmeyer's specimens from Cape Jaubert. Otherwise the colonies and zooids are similar in all respects. The form of the colony, length of the abdomen, and course of the alimentary canal are all characteristic. An examination of Herdman's specimens of *Colella cyanea* in the Australian Museum has shown the species to be identical.

Eudistoma globosum, sp. nov.

Figs. 1 and 2

Records.—Common all around Rottnest I., W.A.

Colony.—Irregularly rounded cylindrical, cushion-shaped, or mushroom-shaped lobes, a maximum of 1 cm in diameter. Lobes rising out of sandy, sometimes stalked and sometimes spreading base. Maximum height of colony 1·5 cm. Sand from the basal portion extending up into centre of fleshy head. Gelatinous but tough test, basal sandy portion colourless, head blackish green. Zooids scattered vertically through test, opening separately to surface.

Zooid.—Maximum length 1 cm. Thorax 0·2 cm long. Branchial aperture terminal on a short 6-lobed siphon; atrial aperture anterodorsal on a siphon twice the length of branchial siphon. Dorsal ganglion conspicuous on outer surface at base of atrial siphon. About 20 longitudinal muscle bands on thorax and continuing along abdomen; about 20 transverse muscle bands on thorax only. Three rows of stigmata with about 25 stigmata in each row. Ten branchial tentacles. Oesophagus very long and narrow; stomach round and smooth, in extreme posterior portion of abdomen. Intestinal gland a tubular structure from lower part of stomach, extending in many parallel branches up rectum. Mid intestine present but no posterior stomach (Fig. 1). One or two developing embryos in peribranchial cavity.

Larva (Fig. 2).—Well-developed embryo 0·9 mm long; 4 ampullae in median line alternating with suckers. Most ventral sucker showing tendency to divide into two.

Discussion.—Both zooids and colony of this species resemble very closely *E. olivaceum* (Van Name) (Berrill 1947) from Florida and the West Indies. This latter species also has a well-developed intestinal gland. In *E. globosum*, however, there are

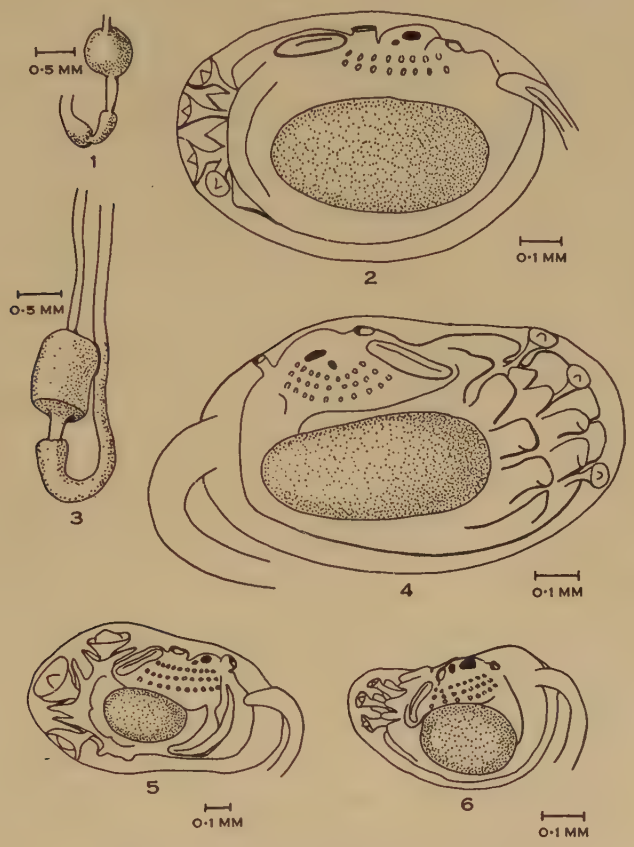

Fig. 1.—*Eudistoma globosum.* Alimentary canal. Fig. 2.—*E. globosum.* Larva. Fig. 3.—*E. arenosum.* Alimentary canal. Fig. 4.—*E. arenosum.* Larva. Fig. 5.—*E. renieri.* Larva. Fig. 6.—*E. pyriforme.* Larva.

fewer branchial tentacles and more stigmata in each row. The zooid is also very similar to that of *E. multiperforata* (Sluiter) from Borneo. It is distinguished, however, by the pigmentation and form of the colony.

Eudistoma arenosum, sp. nov.

Figs. 3 and 4

Records.—Rottnest I., W.A.

Colony.—Rounded, sometimes mushroom-shaped, sand-covered, about 2·5 cm in diameter. Test soft. Sand forming continuous layer on surface interrupted by openings of zooids. Sand particles more sparse below surface. Zooids scattered throughout, opening separately to exterior.

Zooid.—0·8 cm long in relaxed condition. Apertures on short 6-lobed siphons, branchial aperture anterior, atrial aperture anterodorsal. Both siphons directed anteriorly. Thorax 2 mm long. About 20 longitudinal muscle bands on either side of thorax, continuing in 2 bands along either side of ventral aspect of abdomen. Transverse muscles present on thorax. Three rows of stigmata with about 18 stigmata in each row. Stomach fairly large, cylindrical, and smooth, present in posterior part of middle third of abdomen. No differentiation of intestine, which is sharply cut off from rectum (Fig. 3). Gonads of usual form in loop of gut. Gastric gland similar to that of *E. globosum*. Two developing embryos in peribranchial cavity.

Larva (Fig. 4).—Large; the well-differentiated embryo 1·0 mm long. Ampullae at anterior end particularly well developed for this genus. Two rows of ampullae either side of the suckers, with 5 ampullae in each of the most lateral rows, and 4 in each of the median rows. Three rows of stigmata present.

Discussion.—The alimentary canal of the present species, together with the large number of stigmata, distinguish it from others. Unfortunately larvae are not available at stages to determine the origin of the most lateral rows of ampullae; or to establish whether or not these are homologous with those found in a similar position in Polyclinidae. The median paired row is homologous with the median unpaired ampullae in certain Polyclinidae, and with the paired or unpaired ampullae of Polycitorinae; and the tail when wound around the embryo does not intervene between either of these median rows and the suckers. The presence of the 2 rows of ampullae on each side of the suckers is characteristic of the species.

Eudistoma renieri (Hartmeyer)

Fig. 5

Polycitor renieri Hartmeyer, 1912, p. 309.
Eudistoma renieri Michaelsen, 1923, p. 10, for literature and synonymy.

Records.—Point Peron, W.A.

Colony.—One colony only available in the present collection. A flattened cushion, oval in outline with a uniform thickness of 1 cm. Test semi-transparent; zooids regularly spaced, opening separately onto upper surface.

Zooid.—Abdomen only about one-third the length of thorax. Siphons both 6-lobed; branchial siphon short, terminal; atrial siphon about twice the length of branchial and from anterodorsal corner of thorax. Both longitudinal and transverse muscles well developed in body wall of thorax, continuing along siphons. About 10 longitudinal muscle bands and many more transverse bands on thorax. Twelve branchial tentacles; 18 stigmata in each of the three rows. Alimentary canal very similar to that of *E. globosum*. However, the duodenal area is longer in *E. renieri* and there is a mid-intestinal region constricted off from the rectum. This mid-intestinal region, although it holds the same position in relation to the rectum and the duodenum as does the posterior stomach found in other species, has not the compact structure nor the thick muscular walls characteristic of the typical posterior stomach. The intestinal gland is similar to that of *E. globosum*.

Larva (Fig. 5).—Large; only 1 developing embryo present in peribranchial cavity serving as brood pouch. Well-developed embryo measures 1 mm; 3 large

suckers present anteriorly, each surrounded basally by cup-like extensions of ectoderm corresponding to ectodermal ampullae found in other species. An incipient lateral ridge present on each side of embryo, produced into 3 shallow rounded lobes, may correspond to most lateral rows of ampullae in *E. arenosum*. Three rows of stigmata present.

Discussion.—Despite the fact that previous records of this species are from the Cape of Good Hope, the present specimen agrees so well in all aspects that it cannot at present be separated from the South African species. The zooids and the musculature as well as the colony are similar to those of *E. pyriforme* (Herdman); however, the latter species has a distinctive posterior stomach which is not present in *E. renieri*. Hartmeyer (1912) does not indicate the presence of the constriction between the rectum and the mid intestine in his specimens from South Africa; however, this may have been overlooked owing to the presence of food in the gut. *E. ovatum*, which Michaelsen (1921) suggests may be a synonym of the present species, is distinguished by the alimentary canal and the thoracic musculature. The larval form of the present specimen is distinctive, and when available the larvae of the South African specimens may distinguish the two forms.

Eudistoma angolanum Michaelsen

Polycitor (*Eudistoma*) *paessleroides* var. *angolana* Michaelsen, 1914, p. 430.
Eudistoma angolanum Millar, 1953, p. 280, for literature and synonymy.

Records.—Cape Boileau, W.A. (Hastings 1931); Cape Jaubert, W.A. (Hartmeyer 1919); Cape Naturaliste and Green Pools, W.A.

Discussion.—These specimens agree with all previously described members of the species. They differ from *E. snakabri* Tokioka (Tokioka 1954*a*) only in the form of the colony, the pigmentation of the test, and the number of stigmata in each row. Unless these are shown to be variable characters, these two very similar species must remain separate.

Eudistoma pyriforme (Herdman)

Fig. 6

Psammaplidium pyriforme Herdman, 1886, p. 419.
Eudistoma pyriforme Hastings, 1931, p. 84, for literature and synonymy.

Records.—Port Noarlunga, S.A.; Great Barrier Reef (Hastings 1931).

Colony.—As previously described by Herdman and redescribed by Hastings (1931).

Zooid.—As previously described. Proximal part of rectum takes an S course. As Hastings has remarked, the extent to which the course of the alimentary canal is curved is probably dependent upon the degree of contraction of the abdomen. There is, however, in these specimens the characteristic long narrow duodenal region and the oval posterior stomach in the loop of the gut. The stomach itself is well anterior to the posterior end of the abdomen. The mantle musculature is as described by Hastings (1931) and is useful in distinguishing this species from the closely related *E. ovatum* (Herdman) which has only 4–6 longitudinal muscle bands on the thorax.

Larva (Fig. 6).—Maximum length 0·5 mm. The usual 3 anterior suckers present. Two pairs of ampullae opposite the spaces between the suckers, also pairs of ampullae dorsal and ventral to the suckers. Tail in earlier embryo wound around to the right of suckers and ampullae. It does not seem possible, therefore, that these ampullae are homologous with the lateral paired ampullae of certain species of Polyclinidae; it seems rather that their origin is similar to that of the median unpaired ampullae of certain species of Polycitorinae.

Discussion.—This species is distinguished from others with well-developed siphonal musculature by the number of longitudinal muscle bands on the thorax and by the form and course of the alimentary canal. For although Hastings (1931) suggests that the coiling of the alimentary canal may be the result of the contraction of the zooid it is significant that it does occur invariably in zooids of this species and is not observed in the zooids of other species which make other provisions to accommodate the alimentary canal when the zooid is contracted.

Eudistoma fantasiana, sp. nov.

Figs. 7 and 8

Records.—Reevesby I., S.A. (north end of peninsula; McCoy Expedition).

Colony.—Flat, investing, of 1 cm maximum breadth, 4·0 mm thick. Test soft, transparent, with black pigment scattered throughout.

Zooid.—Opening separately to surface. Length 3·0 mm. Thorax one-third of total length. Apertures anterior, 6-lobed, on very short siphons. Branchial siphon terminal, atrial siphon anterodorsal. About 16 longitudinal muscle bands and numerous transverse muscles on thorax. Longitudinal muscles continue along abdomen on right and ventral aspects, not on the left. Muscles on abdomen not concentrated into bands. Three rows of about 18 stigmata. Oesophagus of medium length, opening into large smooth spherical stomach in posterior third of abdomen. Duodenal area very short (Fig. 7), a small spherical posterior stomach, and a short mid-intestinal area opening into rectum. Proximal part of rectum forms loop of gut. Gonads of usual form, but testes lobes particularly numerous, both in gut loop and scattered over left side of gut. Usually 1 large embryo and 1 or 2 eggs in brood pouch, which is constricted off from atrial cavity.

Larva (Fig. 8).—Huge, spherical, about 1·5 mm in diameter. Notable for absence of usual 3 suckers anteriorly. Instead there are 2 dorsoventrally elongate organs with parallel cylindrical cells vertical to their free edge and surrounding a central concavity. Small ampullae present at base of these modified suckers, 1 pair ventrally, and single ampullae on right between suckers, 2 on left and 1 median dorsal.

Discussion.—Therefore, although this species has similar thoracic musculature to many other species of the genus, it is a particularly specialized form and is characterized by the abdominal musculature, the form of the alimentary canal, the form of the brood pouch, and the form and size of the larva.

Eudistoma parvum (Oka)

Fig. 9

Distoma parvum Oka, 1927, p. 497.
Eudistoma parvum Tokioka, 1954*b*, p. 72, for literature and synonymy.

Records.—Long Reef, N.S.W.

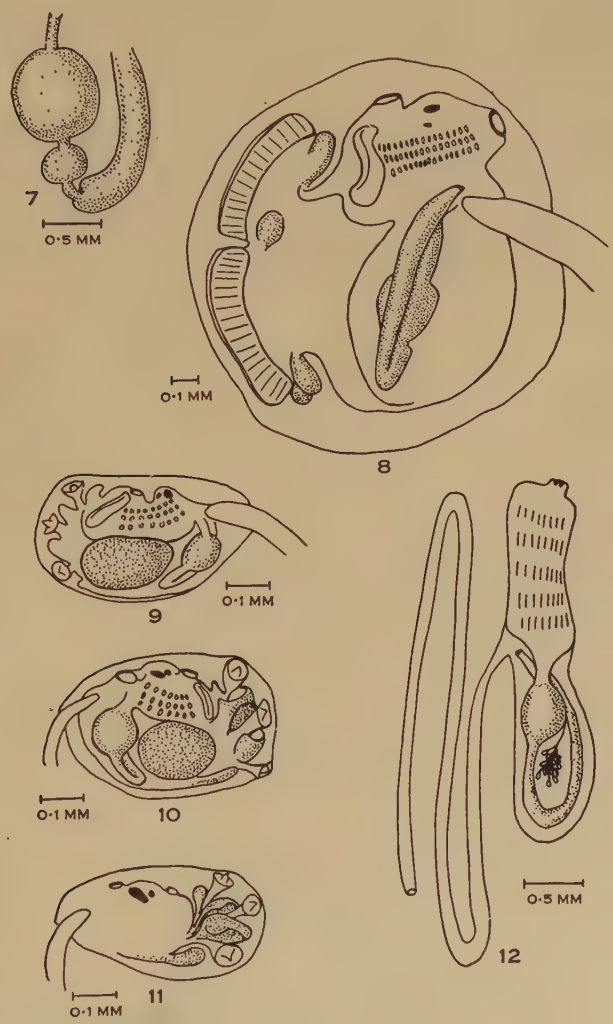

Fig. 7.—*Eudistoma fantasiana.* Alimentary canal. Fig. 8.—*E. fantasiana.* Larva. Fig. 9.—*E. parvum.* Larva. Fig. 10.—*E. elongata.* Early larva. Fig. 11.—*E. elongata.* Late larva. Fig. 12.—*Polycitor longitubis.* Zooid.

Colony.—One small pillar-shaped colony, 1·5 cm high. Zooids plentiful, visible through transparent test of head and stalk.

Zooid.—5·0 mm long. Thorax 1·0 mm in length. Opening separately on surface of colony by 2 short 6-lobed siphons. About 12 longitudinal muscles on

thorax and about 20 transverse muscles superficially. Three rows of stigmata with 18 stigmata in each row. Oesophagus long, opening into smooth-walled spherical stomach in posterior part of abdomen. A short mid intestine; a small oval posterior stomach in loop of gut. Gonads of usual form, present in loop of gut. One to 4 developing embryos in peribranchial cavity.

Larva (Fig. 9).—Only about 0·5 mm long. Of typical form for this genus, with 3 anterior suckers and median unpaired ampullae dorsally, ventrally, and between the suckers.

Discussion.—The small size of the zooid and larva and the form of the colony distinguishes this form from others with similar thoracic musculature and alimentary canal. The species is, however, very similar to *Archidistoma parva* (Sluiter), from Laysan, but has not the characteristic elevation of the test over the anterior portions of the zooids. Nor has Sluiter's species a posterior stomach; and it has many fewer stigmata than *E. parvum*.

Eudistoma elongata (Herdman)

Figs. 10 and 11

Colella elongata Herdman, 1886, p. 110.

Records.—Mud flats, Cronulla and Shell Point, N.S.W.; Port Jackson, N.S.W. (Herdman 1886); Dunwich, Currumbin, Qld.

Colony.—Clumps of club-shaped lobes with narrow stalks from a common base. Smallest lobes about 2·0 cm long, widest portion of head 1·0 cm in diameter; largest about 7·0 cm long, without very appreciable increase in diameter. Zooids plentiful, crowded in semi-transparent test with openings all around head; abdomens project posteriorly into centre of head, while those zooids around base of head may project posteriorly into stalk.

Zooid.—About 6–10 mm long. Thorax only 1 mm in length. Apertures both 6-lobed on short siphons. Branchial siphon terminal, atrial siphon anterodorsal. Mantle musculature well developed with about 20 transverse muscle bands and 16 fine longitudinal muscles continuing along the abdomen. Three rows of stigmata with 14–16 stigmata in each row. Oesophagus long; a round smooth stomach present in posterior third of abdomen. A duodenal area, a small oval posterior stomach, and mid intestine present, the latter opening into rectum in loop of gut. Up to 6 developing embryos in atrial cavity on right side of branchial sac.

Larva (Figs. 10 and 11).—Small, about 0·5 mm long. Four well-developed ampullae present in mid line: 1 dorsal, 1 ventral, and 2 between the suckers. Ampullae between suckers grooved on dorsal and ventral aspects to accommodate stalk of suckers. As usual, ampullae first arise from a broad base which narrows as embryo develops.

Discussion.—Colonies of this species are of quite distinctive shape; and the crowding of the zooids is also characteristic. The colonies and zooids are slightly similar to those of *E. rhodopyge* (Sluiter), from south-east Africa. However, the alimentary canals and branchial sacs differ.

Genus SIGILLINA Savigny

Three rows of stigmata; zooids completely enclosed in common test; stomach folded.

Key to Species of Sigillina

1. Colony stalked ..... *S. australis* Savigny
   South-west Australia (Michaelsen 1930)
   Colony not stalked 2
2(1). With 4 stomach folds ..... *S. magalhaensis* (Michaelsen)*
   Red Sea, Seychelles, Western Australia
   With more than 4 stomach folds ..... *S. psammophorus* (Hartmeyer)
   South Africa (Hartmeyer 1912)

Sigillina magalhaensis (Michaelsen)

Paessleria magalhaensis Michaelsen, 1907, p. 69.
Sigillina magalhaensis Michaelsen, 1930, p. 492, for literature and synonymy.

Records.—Houtman's Abrolhos, W.A. (Michaelsen 1930); Rottnest I. and Point Peron, W.A.

Colony.—Irregular, more or less circular cushions, 1 cm thick and 3 cm in diameter. Base and sides thickly embedded with sand grains extending through the whole test. Central area of upper surface free from sand. Zooids in systems around common cloacal openings, which are large, numerous, with pronounced lips, and arranged in long furrows in the sand-free portion of upper surface of colony. Zooids occasionally black; sometimes black pigment also present in test.

Zooid.—8 mm long of which thorax is 2 mm. Branchial siphon terminal; atrial siphon about twice length of branchial, arising from dorsal surface of zooid opposite 1st row of stigmata. The most anterior atrial lobes may be longer than others (Michaelsen 1930). A prominent dorsal ganglion visible externally at base of atrial siphon. Strong transverse and longitudinal muscles on thorax, both extending along long atrial siphon. Longitudinal muscles also continue in bands along abdomen. Three rows of stigmata with 18–20 stigmata in each row; those in 1st row reduced in length ventrally. Oesophagus long, stomach in posterior third of abdomen. Folds of stomach wall only observed with difficulty; sometimes 4 lines down the stomach where the walls are thinner are the only indications of folds. A duodenal area, a round posterior stomach in loop of gut, and a mid-intestinal region all present. Gonads in loop of gut distinctive in particularly large size of testes lobes.

Discussion.—In the development of musculature on the body wall and siphons and in the course of the alimentary canal, this species is very similar to *E. pyriforme* (Herdman). Tokioka (1950) has described specimens of the latter species from Japan with the same ventral reduction in length of the stigmata in the 1st row. The arrangement of zooids in the colonies, however, serves as a distinguishing character. Van Name (1945, p. 132) has discussed this species as a member of the genus *Polycitor*, basing this on the uncertainty, in previous descriptions, of the number of rows of stigmata in the branchial sac. In the present specimens, however, despite the contraction of the thorax, there are definitely only 3 rows of stigmata; and although stomach folds are indistinct, the stomach wall is invariably thinner in the region of these folds. Thus the species is here retained as a member of the genus *Sigillina*.

Genus POLYCITOR Renier

Indefinitely numerous rows of stigmata; stomach folded.

Key to Species of Polycitor

1. Atrial aperture with 3 anterior lips only ..... *P. violaceus* Sluiter†
   East Indies (Sluiter 1909)
   Atrial aperture 6-lobed 2
2(1). With 4 rows of stigmata ..... *P. spirifer* Sluiter
   East Indies (Sluiter 1909)
   With more than 4 rows of stigmata 3
3(2). With less than 10 rows of stigmata 4
   With more than 10 rows of stigmata 7
4(3). Atrial siphon from opposite last row of stigmata ..... *P. longitubis*, sp. nov.*
   South-west Australia
   Atrial siphon from anterior to last row of stigmata 5
5(4). Posterior stomach present ..... *P. translucida*, sp. nov.*
   Point Peron and Fremantle, W.A.
   Posterior stomach not present 6
6(5). Abdomens of zooids separated from one another in basal root processes
   ..... *P. subarborensis*, sp. nov.*
   Brush I., N.S.W.
   Abdomens of zooids not separated ..... *P. signiferus* Sluiter
   East Indies (Sluiter 1909)
7(3). Smooth stomach ..... *P. aurantiacus* (Herdman)
   North-west Australia, Bass Strait (Hartmeyer 1919)
   Stomach with folds 8
8(7). Stomach with 4 folds 9
   Stomach with more than 4 folds 10
9(8). Twelve longitudinal muscles on thorax ..... *P. gelatinosa*, sp. nov.*
   Rottnest I., W.A.; South Australia
   More than 12 longitudinal muscles on thorax ..... *P. giganteum* (Herdman)*
   Victoria, New South Wales
10(8). Male gonad a thick tube ..... *P. renzi-wadae* Tokioka
   Arafura Sea (Tokioka 1952)
   Male gonad not a thick tube 11
11(10). Ten to 12 stigmata in each row ..... *P. nitidus* (Sluiter)
   South-west Africa (Hartmeyer 1912)
   More than 30 stigmata in each row ..... *P. circes* Michaelsen*
   Western Australia

Polycitor longitubis, sp. nov.

Fig. 12

Records.—The type specimen only is available; from a collection in the Zoology Department of the University of Western Australia labelled "West Australian Beaches". It has been ascertained that these collections were made from beaches in the south-west of Western Australia, from Albany to Fremantle. Unfortunately no more precise location can be given.

Colony.—Flattened cushion, 6 cm in diameter, 1 cm high. A depression present around the upper surface, over which the sides of the colony are folded in toward

† From Sluiter's description this species has characteristics which conform with those of Holozoinae rather than Polycitorinae.

the centre. In some places, flaps of test bearing zooids from the central area of the upper surface are folded over the depression toward the periphery of the colony. Test gelatinous, semi-transparent. Zooids present only around the borders of the colony on either side of the depression mentioned above.

Zooid (Fig. 12).—3 mm long; thorax and abdomen of equal length. Branchial opening 6-lobed, on a very short siphon opening into depression around borders of the colony. Thus zooids in flaps covering depression open on under surface of flap. Immensely long and narrow atrial siphon, the main feature of this species, rising from opposite last row of stigmata, directed immediately posteriorly to open on opposite surface to branchial opening. Therefore, those zooids in flaps of tissue covering depression have shorter atrial siphon opening on upper surface of colony. No lobes were detected fringing atrial siphon. Five rows of stigmata with about 8 stigmata in each row. Oesophagus short, stomach small and smooth; intestine undifferentiated; rectum opening into proximal end of atrial siphon. A group of about 12 testes lobes in loop of gut. An ovary not detected in the colony.

Discussion.—This species is distinguished from all others by the position and length of the atrial siphon, the short oesophagus, small stomach, and number of rows of stigmata.

Polycitor translucida, sp. nov.

Fig. 13

Records.—Reef undercut, Point Peron; hull of F.V. *Bonthorp* in Fremantle Harbour, W.A.

Colony.—Small, cylindrical, 2 cm high. Basal half covered with sand; distal part slightly expanded, free from foreign matter. Zooids visible through glassy test.

Zooid.—Occupying most of length of colony, opening separately on upper surface. About 12 zooids in lobe. Thorax only 2 mm long, most of body length occupied by abdomen. Apertures both 6-lobed on short siphons; branchial aperture terminal, atrial aperture anterodorsal. About 8 rows of stigmata with 20 stigmata in each row. Oesophagus long; stomach cylindrical with 4 longitudinal folds, and is present in posterior third of abdomen. An egg-shaped posterior stomach in pole of intestinal loop. Gonads of typical form present in gut loop posterior to stomach.

Larva (Fig. 13).—Small, 0·5 mm long, of type with median ampullae alternating with suckers. All ampullae except the ventral one divide into two in the late embryo.

Discussion.—This species is distinguished from others in this and neighbouring localities by the size of the zooid and colony, the presence of a posterior stomach, and the comparatively few rows of stigmata in the adult.

Polycitor subarborensis, sp. nov.

Fig. 14

Records.—Brush I., 45 fm, off Ulladulla, N.S.W.

Colony (Fig. 14).—A spherical head 1 cm in diameter, a basal sand-covered portion corresponding to stalk, broken up into spreading root-like processes. Test

of head firm, gelatinous, and semi-transparent. Zooids extend through head, and each terminal branch of root-like processes accommodates posterior portion of 1 zooid.

Zooid.—1·5 cm long, thorax 2 mm in contracted state. Apertures on very short 6-lobed siphons, terminal and anterodorsal respectively, opening separately to exterior. Atrial opening toward centre of colony. Twelve longitudinal muscle bands on thorax continuing along abdomen in 4 wide bands. Nine rows of long stig-

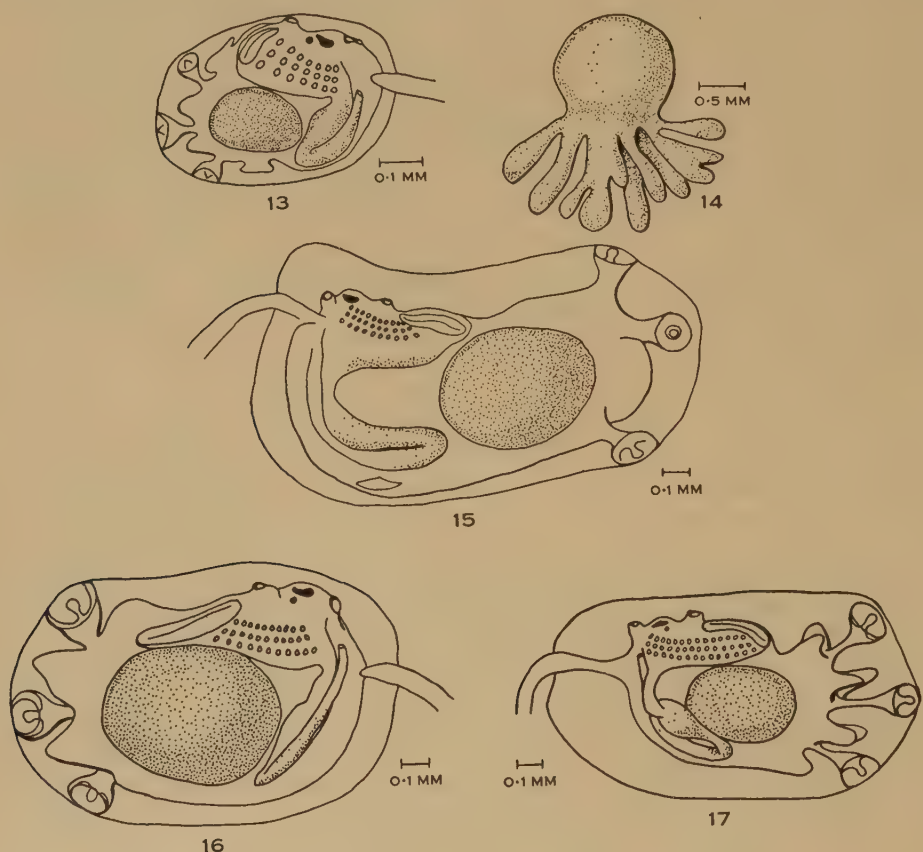

Fig. 13.—*Polycitor translucida.* Larva. Fig. 14.—*P. subarborensis.* Colony. Fig. 15.—*P. gelatinosa.* Larva. Fig. 16.—*P. giganteum.* Early larva. Fig. 17.—*P. giganteum.* Late larva.

mata with about 30 in each row. Oesophagus long, opening into squarish stomach with 4 longitudinal thickenings. Stomach in posterior part of abdomen. No posterior stomach present. Gonads in gut loop.

Discussion.—The separation of the abdomen of zooids in their own test, which acts as roots to anchor the colony, is quite distinctive. Although this modification is probably of a secondary nature, it has not been observed before in any species of any genus; and its existence here is considered sufficient to separate the colony as representing a distinct species.

Polycitor gelatinosa, sp. nov.

Fig. 15

Records.—Rottnest I., W.A.; Port Noarlunga, S.A.

Colony.—Cylindrical, fan-shaped, or rounded lobes, 2–5 cm wide, 2 cm thick, 3 cm high. Test soft, gelatinous, semi-transparent. Zooids radiating out from narrow base into head, opening separately on surface. Systems not evident.

Zooid.—0·5–1 cm long. Thorax only 0·2 cm long. Apertures both 6-lobed, on very short siphons; branchial aperture terminal, atrial aperture anterodorsal. About 12 longitudinal muscle bands on each side of thorax, continuing along abdomen and along a short posterior abdominal extension. Twelve to 16 rows of stigmata with 20–30 stigmata in each row. Oesophagus long and wrinkled. In South Australian specimens, stomach long with 4 folds; in the specimens from Rottnest I., inner stomach wall broken up into papillae arranged in 20 longitudinal rows. Stomach always present in posterior third of abdomen. Ten lobes fringing anus. Up to 3 developing embryos in distal part of brood pouch, just posterior to thorax; only one of these embryos is ever well developed.

Larva (Fig. 15).—Very large, about 1·7 mm long, resembling larva of *Pycnoclavella aurilucens* (see Berrill 1950) in lack of ampullae between suckers and in enormous development of anterior region.

Discussion.—The minute papillae arranged in rows in the stomach of specimens from Rottnest I. are not considered a sufficient character on which to separate specimens from the two localities. The species resembles *P. giganteum* (Herdman) from the south-eastern coast of Australia in all characters except the size of the colony, the texture of the test, and the number of longitudinal muscles on the thorax. The larvae are quite distinct from those of other species of *Polycitor*.

Polycitor giganteum (Herdman)

Figs. 16 and 17

Polyclinum giganteum Herdman, 1899, p. 79.
Polyclinum globosum Herdman, 1899, p. 80.
Nec *Polycitor giganteus* Sluiter 1919, p. 10 = *Diazona giganteum* (Sluiter).

Records.—17–24 fm, Lakes Entrance, Vic.; Balnarring beach, North Brighton reef (Melbourne), Vic.; Jervis Bay and Port Jackson, N.S.W.

Colony.—Varying from stalked spherical forms to unstalked spherical or oval forms, or smaller flat-topped colonies with very narrow base. Test of large stalked specimens from Jervis Bay, of a smaller flat-topped colony from North Brighton reef, and of a large spherical colony from Lakes Entrance, clear and glassy with zooids completely visible in test. Other colonies with semi-transparent test. Largest colonies spherical, 7 cm in diameter, from Port Jackson and Lakes Entrance. Smallest colony from North Brighton reef with a flat upper surface about 3 cm in diameter, fixed by very narrow base. Surface of test completely smooth, without sand. Stalk or base of colony may have coating of sand. Zooids opening separately to surface, sometimes crossing one another in test. Abdomens of zooids extending down into stalk when that is present.

Zooid.—Size depending directly on size of colony, from 1 cm to 3 cm in length. Thorax only 5 mm. Apertures both on short siphons terminal and anterodorsal respectively. Eighteen longitudinal muscle bands on thorax continuing along abdomen as 8 separate bands. Ten to 16 rows of stigmata with about 30 stigmata in each row. Oesophagus long, opening into stomach in posterior third of abdomen. Stomach more or less rectangular with 4 distinct folds. A short duodenal area separated from rectum by constriction in loop of gut. No true posterior stomach. Anus opening at base of thorax, fringed by 12 distinct lobes. Gonads in loop of gut; numerous testes lobes extend to cover sides of gut. Developing eggs and embryos present in peribranchial cavity. In smaller zooids up to 3 eggs and embryos in peribranchial cavity, in larger zooids sometimes as many as 6 arranged in double row.

Larva (Figs. 16 and 17).—About 1·3 mm long. In earlier embryo median ampullae present alternating with suckers (Fig. 16); in later embryo (Fig. 17) these develop into paired ampullae, except the ventral ampulla, which remains single.

Discussion.—There is a tremendous variation in the form of the colony of this species. The zooids and larvae, however, remain particularly constant, and no characters have been observed which could distinguish any of the variations as distinct species. The species is closely related to *P. crystallinus* Renier (Carlisle 1953) from the Mediterranean, from which it may be distinguished only by the size of the colony and larva. The present species is not related to *P. giganteus* Sluiter from the East Indies, which Arnback has shown to be a species of *Diazona* (see Van Name 1945, p. 156).

Polycitor circes Michaelsen

Polycitor circes Michaelsen, 1930, p. 495.

Records.—35–37 fm, Cape Inscription, W.A.; Shark Bay and Fremantle, W.A. (Michaelsen 1930).

Colony.—Large, almost club-shaped, 7 cm wide on upper surface, narrowing toward base; 9 cm high. A zooid-free area, about 1 cm high in narrow basal portion serving as stalk fixing colony. Test soft, gelatinous, almost opaque. Zooids opening separately to surface all around head.

Zooid.—About 1–1·5 cm long. Branchial aperture on very short siphon terminally; atrial siphon similar, anterodorsally. Sixteen longitudinal muscles from base of branchial siphon running slightly obliquely, the more ventral ones joining into bands along either side of endostyle; these bands are joined by more dorsal muscles at base of thorax to form 2 bands running along ventral side of abdomen. Dorsally on thorax, 7 longitudinal muscle bands from around base of atrial siphon curve dorsally behind it and continue along dorsal surface of abdomen. Seventeen rows of very short stigmata with wide transverse vessels between each row and 35 stigmata in each row. Stomach in posterior third of abdomen with 25 fine longitudinal ridges particularly marked internally. A very long blood-vessel from end of abdomen extending down into stalk of colony.

Discussion.—Michaelsen (1930) has not remarked on the shortness of the stigmata, and his specimens have more rows of stigmata and fewer stomach folds.

These characters are, however, variable to a certain extent. The specimens are identical in all other ways.

Genus POLYCITORELLA Michaelsen

Polycitorinae with spicules in the test.

No species of this genus have yet been taken in Australia. The following species, however, occur in the areas indicated.

Key to Species of Polycitorella

With 3 rows of stigmata ..... *P. mobiusii* (Hartmeyer)
West Africa (Michaelsen 1923)
With 12 rows of stigmata ..... *P. mariae* Michaelsen
North Island, New Zealand (Michaelsen 1924)

Subfamily CLAVELININAE

Genus CLAVELINA Savigny

Zooids free and embedded; stomach folded.

Key to Species of Clavelina

1. Three rows of stigmata ..... *C. diminuta*, sp. nov.*
Rottnest I., W.A.
More than 3 rows of stigmata 2
2(1). Zooids separate ..... *C. enormis* Herdman*
Red Sea, Indian Ocean, Western Australia
Zooids enclosed in common test 3
3(2). Transverse muscles distinct; 20 stigmata in each row ..... *C. arafurensis* Tokioka
Arafura Sea (Tokioka 1952)
No transverse muscles; 40–50 stigmata in each row 4
4(3). More than 10 rows of stigmata ..... *C. baudinensis*, sp. nov.*
Rottnest I., W.A.; Victoria
Less than 10 rows of stigmata ..... *C. claviformis* (Herdman)*
New South Wales

Clavelina enormis Herdman

Fig. 18

Clavelina enormis Herdman, 1880, p. 725. Michaelsen, 1930, p. 474, for synonymy and literature.

Records.—24° 54′ S., 113° 16′ E., toward Point Charles, 9–13 fm, Koks I., W.A.; Oyster Harbour, Albany, W.A. (Michaelsen 1930).

Colony.—Separate zooids fixed by their own test, or joined by a basal stolon. Zooids 8–20 cm long, 1 cm wide anteriorly but narrowing toward the base. Test transparent anteriorly, becoming leathery and opaque posteriorly.

Zooid.—Occupying full length of test; thorax about one-quarter of total length. Branchial aperture terminal, atrial aperture slightly posterior on dorsal surface. About 25 rows of elongate stigmata with about 50 stigmata in each row. Thorax with 17 muscle bands running posterodorsally from ventral surface, continuing along dorsal surface of abdomen in a single band. Oesophagus long, opening into stomach in middle third of abdomen. Stomach small, rectangular due to the 4 folds along its

wall; folds internal, not obvious on outer aspect of stomach. Gonads present in gut loop posterior to stomach; testes lobes particularly numerous; a tubular oviduct packed with eggs. About 100 developing embryos in peribranchial cavity acting as brood pouch.

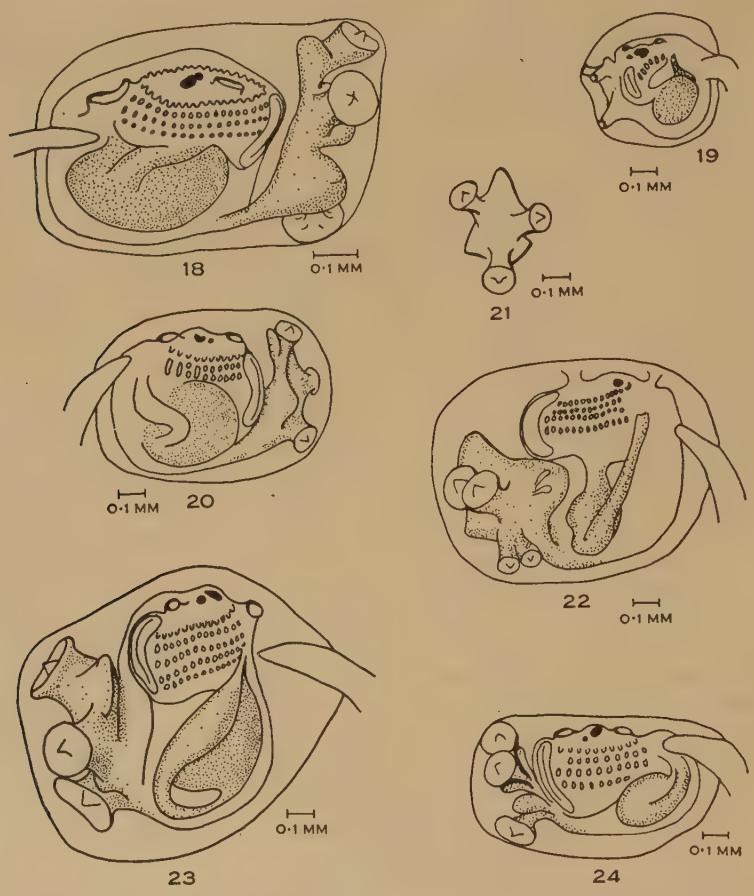

Fig. 18.—*Clavelina enormis*. Larva. Fig. 19.—*C. baudinensis*. Small larva (type colony, Rottnest I.). Fig. 20.—*C. baudinensis*. Large larva (colonies from Rottnest I. and Victoria). Fig. 21.—*C. baudinensis*. Anterior view of sucker-bearing stalk, from large larva. Fig. 22.—*C. claviformis*. Larva. Fig. 23.—*Podoclavella moluccensis*. Larva. Fig. 24.—*P. meridionalis*. Larva.

Larva (Fig. 18).—0·8 mm long. Three large suckers anteriorly on a common stalk from ventral aspect of larva. These suckers have a triradiate arrangement so that the most dorsal is slightly to the left, middle sucker inclined to the right, and ventral sucker directed ventrally. In well-developed embryo, single ampullae present at base of each sucker, on side opposite to that in which the sucker is developed. Ampullae increase in length as embryo develops. Four rows of about 18 stigmata, of which the most anterior row is apparently newly differentiating stigmata.

Discussion.—This species is very similar to *Podoclavella meridionalis* Herdman. However, whereas the present species has an Indian Ocean–Western Australian distribution *P. meridionalis* is found principally along the east coast of Australia. The 2 species are further distinguished by different proportions of the zooid; and the stomach in each is quite distinctive.

Clavelina baudinensis, sp. nov.

Figs. 19–21

Records.—Reef undercuts, Rottnest I., W.A.; Balnarring beach and Laverton Bay, Vic.

Colony.—A gelatinous translucent head on firm stalk. Total length 3·5–8 cm, diameter of head 1–1·5 cm. Stalk usually slightly longer than head, diameter decreasing with increasing length. Several colonies from Rottnest I. with thoraces of zooids enclosed in their own discrete layer of test, projecting varying distances from common test; thus giving colony arborescent appearance with primary and secondary branches. One specimen with shorter, broader stalk has head fanning out so that whole colony is rather mushroom-shaped. Other colonies, however, with head scarcely of greater diameter than stalk. Thoraces and necks of zooids in soft test of head; abdomen in harder test of stalk.

Zooid.—Both apertures opening separately, smooth-rimmed on very short siphons. Branchial aperture terminal, atrial aperture slightly dorsal in contracted state. In extended zooid branchial aperture turns ventrally, atrial aperture then becomes terminal. Thorax about one-third length of abdomen; total length of zooid about 2 cm. Only weak musculature, confined to about 12 fine longitudinal bands on either side of thorax and continuing down along abdomen. Eighteen to 20 rows of long stigmata with 40–50 stigmata in each row and broad horizontal membranes between the rows. Oesophagus long; stomach in posterior third of abdomen in relaxed zooid. In contracted zooid, however, greatest shortening where oesophagus and rectum form neck, and stomach then present in posterior half of abdomen. Stomach squarish with 4 folds, although when extended there are 5 apparent folds. A mid-intestinal enlargement some distance beyond stomach, constricted off from rectum in pole of gut loop. Anus opens at posterior end of thorax. Testes lobes pear-shaped, numerous, present between and around gut loop. Ovary represented by very numerous eggs passing up tubular oviduct. Up to 30 developing embryos may be present in peribranchial cavity.

Larva (Figs. 19–21).—Two distinct types. Smaller type occurring in type colony from Rottnest I., and in several other colonies from that area. Larger type more common, occurring both in those specimens from Rottnest I. with projecting thoraces, and in colonies with zooids completely enclosed in common test; they are also present in specimens from Laverton, Vic. Therefore, on adult characters or on distribution, it has been impossible to separate the specimens into 2 species based on these 2 distinct larval types. The smaller larvae (Fig. 19) 0·5 mm long, with 3 suckers anteriorly. These suckers are not of the usual cup form with central cells but are composed of numerous spindle-shaped cells at right angles to the flat free end of the

sucker. Suckers have usual triradiate arrangement with 1 ventral and 2 dorsally; the latter 2 inclined to right and left respectively. Larger larvae (Fig. 20) 0·9 mm long. Suckers always of the usual cup form with central cells, and the anterior extension of the larva which bears these suckers is broad and flat, developing an extension dorsally and to right and left of the ventral sucker (Fig. 21). These extensions correspond to the ampullae of other species and do not occur at all in the smaller type of larva. Three rows of stigmata present, the 2 posterior rows apparently arising by the division of 1 row, while the anterior row is differentiating from the anterior part of the branchial sac. In some of the larvae from the Laverton specimens the right dorsal suckers may be divided into two.

Discussion.—The colony of this species is most closely related to *Clavelina arafurensis* Tokioka (Tokioka 1952) from the Arafura Sea. The zooids, however, are distinct in their proportions, in the arrangement of thoracic musculature, and in the branchial sac. The zooid is similar to that of *Clavelina claviformis* (Herdman) from Port Jackson, N.S.W., and from New Zealand. However, in the latter species there are fewer rows of stigmata, and zooids are arranged in rows along the side of the head, whereas in *C. baudinensis* the zooids open onto the flat upper surface of the head. Those colonies where the thoraces project are similar to *Podoclavella cylindrica* Quoy & Gaimard. However, again they are distinguished by musculature, branchial sac, and the stomach. The condition of the larvae in the present species is confusing since the different larvae do not correspond with the variations in the form of the colony, nor with their geographic distribution; the form of the zooids themselves in all specimens is most constant. It may be found that actually 2 species are involved, but for the present, in the absence of any distinguishing characters in the adults, the available specimens have been considered as one species only. The larger larvae are very similar in size and form to those of *O. fascicularis* (Drasche) (see Tokioka 1952, p. 101), but the colony and zooids are distinct.

Clavelina claviformis (Herdman)

Fig. 22

Coletla claviformis Herdman, 1899, p. 67.
Amaroucium anomalum Herdman, 1899, p. 76.
Oxycorynia sigillaria Michaelsen, 1924, p. 269.

Records.—Port Jackson, N.S.W.

Colony.—As described by Herdman (1899).

Zooid.—3–4 mm long with smooth-rimmed apertures opening separately to surface. Thorax and abdomen of equal length in contracted zooid; 12 longitudinal muscle bands on thorax each breaking up into about 6 narrow bands on abdomen. Eight rows of stigmata with about 50 stigmata in each row. Stomach spherical with 4 folds; Herdman's "numerous" folds probably due to collapsed condition of his specimens. Gonads present in loop of gut.

Larva (Fig. 22).—1 mm long. Sucker stalk anteriorly forming flattened plate very much wider than the same structure in larger larvae of *C. baudinensis*. Suckers rising from the centre of this plate with usual triradiate arrangement. Ventral sucker often divided into two. Accessory ampullae present at base of suckers.

Discussion.—Herdman states that this species is evidently very abundant on some parts of the Australian coast. It is probable, however, that the ascidian he mentions covering rocks at Roebuck Bay, W.A., is *Eudistoma cyanea*, described above from Rottnest and Triggs Is. in Western Australia and from north-west Australia (Hartmeyer 1919). The colony of the latter species closely resembles *C. claviformis* and is, in the field, the "smoky grey upon which the ends of the zooids show as bright cobalt blue" described by Saville-Kent in a letter to Herdman. *C. claviformis* has not been taken from Western Australia and its distribution, therefore, is possibly confined to the east coast of Australia. Michaelsen's (1924) species *Oxycorynia sigillaria* from New Zealand agrees in every aspect of colony and zooid and is apparently synonymous with the present species. *A. anomalum* Herdman differs only from other specimens in the dimensions of the colony.

Clavelina diminuta, sp. nov.

Records.—Shallow reef undercut, Rottnest I., W.A.

Colony.—Each zooid enclosed in separate test, joined basally by common test. Test material firm, gelatinous, and translucent, except the soft, fragile transparent terminal 4 mm accommodating thoraces.

Zooid.—2 cm high, occupying free test and not extending into basal test material. In contracted zooid thorax twice as wide as its length; thorax length one-fifth of whole zooid. Extended thorax longer than wide; atrial aperture here located terminally owing to oblique orientation of thorax. Width of neck and abdomen 1·5 mm at thickest part in posterior third of abdomen. Apertures both on short smooth-rimmed siphons, branchial aperture terminal and atrial aperture anterodorsal on relaxed thorax. Twenty longitudinal muscles on thorax joining into wide bands on either side of abdomen. Twelve long, simple tentacles extending beyond border of siphon in contracted specimens; long tentacles alternating with shorter ones. Three rows of very elongate stigmata with 35 stigmata in each row. Dorsal lamina represented by 3 large languets. Oesophagus long, opening into rectangular stomach in posterior half of body. Stomach wall with 4 folds particularly marked internally. On dorsal side of abdomen just anterior to stomach and slightly smaller is a large egg at varying distance up oviduct. Testis and ovary of usual form in loop of gut.

Discussion.—The branchial sac and thoracic orientation of the extended zooid of this species more closely approaches *Podoclavella detorta* (Sluiter) than any other species. The thoracic orientation, however, changes according to the degree of extension of the thorax, and normally both apertures are anterior. The present species also is distinguished by 3 rows of stigmata instead of 4; and the stomach folds are distinct. Nor is there here a great extent of zooid-free stalk. The egg is particularly large in relation to the size of the zooid. It is possible that the species is closely allied to *Archiascidia neapolitana* Julin (1904), a primitive clavelinid in the Mediterranean.

Genus PODOCLAVELLA Herdman

Zooids free; stomach smooth.

Key to Species of Podoclavella

1. No stalk; species sessile on ventral side ..... *P. polycitorella* Tokioka
   Japan (Tokioka 1954*a*)
   Zooids stalked 2
2(1). Apertures both on dorsal surface ..... *P. detorta* Sluiter
   East Indies (Sluiter 1904)
   Apertures not both on dorsal surface 3
3(2). Branchial sac folded ..... *P. procera* Sluiter
   East Indies (Sluiter 1904)
   Branchial sac not folded 4
4(3). Thorax small; large brood pouch ..... *P. fecunda* Sluiter
   Aru I., Banda (Sluiter 1913)
   Thorax not small; no true brood pouch 5
5(4). Thoracic muscles mainly transverse 6
   Thoracic muscles mainly longitudinal or oblique 7
6(5). Transverse muscles limited to thorax ..... *P. moluccensis* Sluiter*
   East Indies; Malaya; north-west Australia; Rottnest I., W.A.; Great Barrier Reef
   Transverse muscles continue into abdomen ..... *P. meridionalis* Herdman*
   North-west Australia; Port Jackson, N.S.W.; Great Barrier Reef
7(5). Many individuals from 1 stalk 8
   Each individual with separate stalk 9
8(7). Twenty rows of stigmata ..... *P. cylindrica* Quoy & Gaimard*
   Fremantle, W.A.; Bass Strait
   Ten rows of stigmata ..... *P. australis* (Herdman)*
   Port Jackson, N.S.W.
9(7). Muscles confined to thorax ..... *P. coerulea* (Oka)
   Japan (Oka 1934)
   Muscles not confined to thorax 10
10(9). Leathery stalk present ..... *P. ostrearium* Michaelsen
   Albany, W.A. (Michaelsen 1930)
   No leathery stalk ..... *P. dagysa*, sp. nov.*
   Rottnest I., W.A.

Podoclavella moluccensis Sluiter

Fig. 23

Podoclavella moluccensis Sluiter, 1904, p. 5. Hastings, 1931, p. 82, for synonymy and literature.

Records.—Cape Boileau, W.A. (Sluiter 1895); Garden and Rottnest Is., W.A.; Port Lincoln, S.A.; Great Barrier Reef (Hastings 1931).

Colony.—Separate zooids arising from common, sometimes extensive base. Test soft and gelatinous throughout. Free parts of colony 1–4 cm long, zooids entirely occupying these, not extending down into basal test. Basal test very rich in blood-vessels, with developing buds at ends of stolonic vessels extending periphery of colony.

Zooid.—Largest zooids present in centre of colony. Thorax one-third of length of abdomen. Atrial cavity much enlarged, so that atrial aperture on short siphon becomes terminal and branchial siphon is forced toward ventral side of thorax. Mantle musculature on thorax principally transverse bands, anastomosing ventrally and becoming diffuse dorsally in region of enlarged atrial cavity serving as brood pouch. Fine longitudinal muscles extend along thorax into abdomen. About 20 branchial

tentacles of varying size. Twelve to 16 rows of stigmata with about 35 stigmata in each row. Stomach round and smooth, present half way down abdomen.

Larva (Fig. 23).—About 1·2 mm long. The usual 3 suckers arranged in a triangle anteriorly, with ampullary extensions developed around the edge of the sucker-bearing anterior extension, alternating with the suckers. About 5 rows of well-developed stigmata. Suckers particularly large.

Discussion.—Despite confusion which has previously existed regarding the identity of this species, the muscles of the thorax are completely distinctive.

Podoclavella meridionalis Herdman

Fig. 24

Podoclavella meridionalis Herdman, 1891, p. 603. Hastings, 1931, p. 81, for synonymy and literature.

Records.—North-west Australia (Hartmeyer 1919; Hastings 1931); Port Jackson, N.S.W. (Herdman 1899); Mackay, Qld.

Colony.—Separate zooids which may or may not be joined basally.

Zooid.—About 10 cm long. Anteriorly the test transparent and glassy; posteriorly hard and semi-opaque. This latter portion of test forming the stalk with a long posterior extension from abdomen of zooid extending into it. Thorax two-thirds of length of abdomen. Branchial aperture terminal; atrial aperture on dorsal surface about one-third down length of thorax. About 25 transverse muscles curving down into abdomen at both their ventral and dorsal ends. Thirty-three rows of stigmata with about 80 stigmata in each row; numbers of stigmata decrease in anterior and posterior rows. Stomach smooth, half way down abdomen, small and rounded.

Larva (Fig. 24).—0·9 mm long. Ampullae arising from alternate sides of base of suckers are well developed, while common stalk bearing the suckers is slender and not flattened and wide as in other larvae of the Clavelininae.

Discussion.—This species is very like *Clavelina enormis*, but has more muscles, more stigmata in each row, and more rows of stigmata. *C. enormis* also has a longer stalk.

Podoclavella cylindrica (Quoy & Gaimard)

Fig. 25

Polyclinum cylindrica Quoy & Gaimard, 1834, p. 618.
Clavelina cylindrica Michaelsen, 1930, p. 475, for synonymy and literature.

Records.—Rottnest I., W.A.; Fremantle, W.A. (Michaelsen 1930); Victoria (Quoy & Gaimard 1834); Bass Strait (MacDonald 1858).

Colony.—6·5 cm high. Stalk 2 cm long, 2 cm in diameter, terminating basally in root-like extensions by which colony is fixed. Head covered by zooids enclosed in their own discrete test continuous with central core. Test soft, gelatinous, and transparent.

Zooid.—Length from 1 cm terminally to 0·4 cm at base of head; both apertures terminal and smooth-rimmed. Branchial aperture turned posteriorly by lengthening

of dorsal or anterior border so that opening is posteriorly directed; atrial aperture opening anteriorly. Anterior border of branchial opening so enlarged in relation to posterior border that it closes against ventral surface of zooid rather than against ventral lip of branchial opening. Mantle not very muscular; but there are about 25

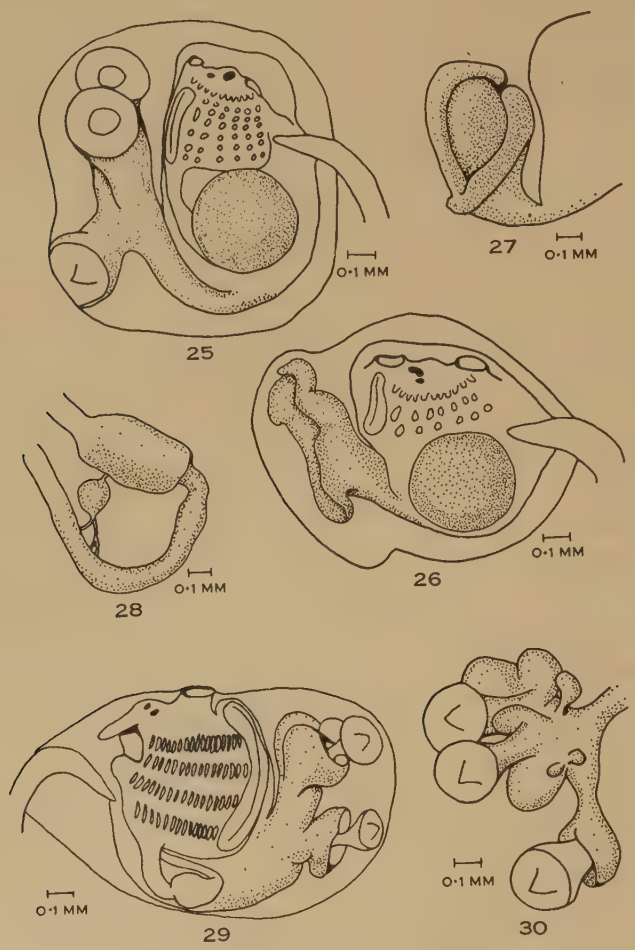

Fig. 25.—*Podoclavella cylindrica.* Larva. Fig. 26.—*P. dagysa.* Larva. Fig. 27.—*P. dagysa.* Anterior view of sucker-bearing stalk. Fig. 28.—*Distaplia viridis.* Alimentary canal showing intestinal gland. Fig. 29.—*D. viridis.* Early larva. Fig. 30.—*D. viridis.* Suckers and ampullae of later larva.

oblique and longitudinal muscle bands branching and anastomosing with one another, confined to the thorax. Twenty-one rows of stigmata with about 40 stigmata in a row. About 6 embryos in a brood pouch formed by an expansion of posterior end of thorax. Abdomen only about three-quarters of length of thorax. Alimentary loop short; a small, smooth-walled, rectangular stomach present.

Larva (Fig. 25).—1 mm long, slightly deeper than long. No development of ampullae from base of suckers. Larva similar to that of *O. fascicularis* (Drasche) (see Tokioka 1952).

Discussion.—Michaelsen's specimens in particular were very much smaller than this one; otherwise his description agrees in all aspects. The present specimen is also identical with those from Victoria and Bass Strait described by earlier authors. Previous authors have, however, described the atrial siphon as turned ventrally; in the present zooids it is the branchial siphon which is turned posteriorly. The zooids, as well as the larvae, are similar to those of *O. fascicularis* also occurring in Western Australia, but is distinguished by the form of the colony and by the branchial sac and thoracic musculature of the zooids. The species may be closely related.

Podoclavella australis (Herdman)

Stereoclavella australis Herdman, 1899, p. 6.

Records.—Port Jackson, N.S.W. (Herdman 1899); Port Denison, Qld. (K3 collection, Australian Museum, E. Allen).

Colony.—The colony from Queensland differs from Herdman's specimen in the basal common test, which here is irregular, creeping along the branches of an alga. Zooids 0·5–1 cm long, free of the common test. Blood-vessels from the zooids ramify and buds develop in the basal test.

Zooid.—In most respects identical with those of *P. cylindrica* but differs in having only 10 rows of stigmata and 12 longitudinal muscle bands.

Larva.—Similar to those of *P. cylindrica.*

Discussion.—This species is so very similar to *P. cylindrica* that they may be geographical varieties of the same species. However, since the numbers of stigmata in the branchial sac and the longitudinal muscles differ, they are for the present considered as 2 species. The colony is also similar to those specimens of *C. baudinensis* where the thoraces become free of the common test.

Podoclavella dagysa, sp. nov.

Figs. 26 and 27

Records.—Shallow undercut reefs, Rottnest I., W.A.

Colony.—Separate zooids joined by basal stolon. Test soft and glassy, may be covered basally with sand. Terminal portion of test free of foreign bodies.

Zooid.—From 1 to 3 cm long; considerably expanded in thoracic region. Both apertures on short siphons, close together and terminal. Branchial siphon turned ventrally. Rim of both siphons minutely serrated. Thorax one-third to one-quarter the length of the whole zooid. Twenty-three fine longitudinal muscle bands on either side of the thorax converging and continuing along the abdomen as a broad muscle band on either side. Few of these muscle bands arise directly from the base of the siphons but they generally run obliquely from the endostyle down into the abdomen. Eighteen branchial tentacles, both long and short alternating. The longer tentacles arising further toward base of siphons. Nineteen rows of rectangular stigmata with about 80 stigmata in each row. Stomach small, smooth, present in posterior third

of abdomen. Numerous testes lobes present in gut loop posterior to stomach; a many-egg ovary superficial to testes on right side of abdomen. Blood-vessels from abdomen ramify out into surrounding test. Many developing eggs and embryos may be present in peribranchial cavity to left of branchial sac.

Larva (Figs. 26 and 27).—1·3 mm long. Particularly remarkable in anterior region where the usual suckers are not present. There is instead a large circular organ with a rounded central projection (Fig. 27). This organ probably has the same function as the suckers.

Discussion.—This species is distinguished from *P. moluccensis* Sluiter by the mantle musculature and by the form and proportions of the body. It resembles *P. meridionalis* Herdman only in the very small stomach. The zooids, the thoracic musculature, and the nature of the test are most closely related to these characters in *Podoclavella cylindrica*. The present species is distinguished from all others, however, by the branchial sac, by the extension of muscles along the abdomen, and by the larva. The specific name is that given, as generic name, to certain species of salps collected by Solander and Banks during Cook's voyages; these salps were described by Solander in a manuscript deposited in the British Museum, Natural History, London. The name was derived from the Greek word meaning "gem", and has been given to the present species because of the clear, glassy nature of the test.

Genus OXYCORYNIA Drasche

Zooids embedded; stomach smooth.

No species of this genus are present in this collection; the following species, however, do occur in the areas indicated:

Key to Species of Oxycorynia

1. Four rows of stigmata ..... *O. centripens* (Sluiter)
   East Indies, Aru I. (Sluiter 1913)
   Ten or more rows of stigmata 2
2. Twenty to 30 long narrow stigmata in each row ..... *O. fascicularis* (Drasche)
   Japan, Philippines, East Indies, Malaya, north-west Australia (Tokioka 1952)
   Ten very small stigmata ..... *O. malayensis* (Sluiter)
   East Indies (Sluiter 1909)

Subfamily **HOLOZOINAE**

Genus DISTAPLIA Della Valle (nomen conservandum)

Four rows of stigmata; atrial aperture with languets; one central or many scattered common cloacal openings.

Key to Species of Distaplia

1. Gonads in sac completely constricted from abdomen 2
   Gonads not in sac completely constricted from abdomen 4
2(1). Parastigmatic vessels present ..... *D. skoogi* Michaelsen
   South Africa (*D. domuncula* Millar, 1955)
   Parastigmatic vessels absent 3

3(2). Zooids in double rows radiating from common cloaca .....*D. australiensis* Brewin*
Southern Tasmania
Zooids not in double rows radiating from common cloaca ....*D. stylifera* (Kowalevsky)*
Red Sea, South Africa, West Indies, north-west and north-east Australia
4(1). Both testes and ovary completely posterior to abdomen .....*D. fasmeriana* Michaelsen
Stewart I. and Otagó Harbour, New Zealand (Brewin 1946)
Testes and ovary not completely posterior to abdomen 5
5(4). With parastigmatic vessels 6
Without parastigmatic vessels 11
6(5). Stomach with internal longitudinal ridges 7
Stomach with internal reticulations 8
7(6). Longitudinal muscle on thorax .....*D. dubia* (Oka)
Japan (Tokioka 1953)
Transverse and oblique muscles on thorax .....*D. vallii* Herdman
Philippines (Van Name 1918)
8(6). Mainly transverse muscles on thorax; 17–18 stigmata in each row 9
Mainly longitudinal muscles on thorax; 12–14 stigmata in each row 10
9(8). Colonies hermaphrodite .....*D. viridis*, sp. nov.*
South Australia
Colonies dioecious? .....*D. domuncula* (Hartmeyer)
South Africa (Michaelsen 1924)
10(8). Gonads never project posterior to intestine .....*D. yezoensis* Oka
Japan (Tokioka 1951)
Gonads project posterior to intestine in mature forms .....*D. occidentalis* Bancroft
Western America (Van Name 1945)
11(5). Four to 6 testes lobes in a rosette .....*D. taylori* Brewin
New Zealand (Brewin 1950*a*)
Ten to 14 testes lobes along vas deferens .....*D. marplesi* Brewin
New Zealand (Brewin 1952)

Distaplia australiensis Brewin

Distaplia australiensis Brewin, 1953, p. 61.

Records.—D'Entrecasteaux Channel, Tas.; southern Tasmania, 24 fm (Brewin 1953).

Colony and zooid.—Both as described by Brewin except for the branchial sac. Brewin has found 22–24 stigmata in each row of the branchial sac; in the present specimens, however, there are only 10–15 stigmata in each row. Brewin's specimens in the Australian Museum have 15–20 stigmata in each row.

Discussion.—It is apparent that, since all specimens examined were fully developed, there is considerable variation in the number of stigmata in the branchial sac in this species. The main distinction, therefore, between this species and *D. stylifera* is in the form of the colony.

Distaplia stylifera (Kowalevsky)

Didemnum styliferum Kowalevsky, 1874, p. 43.
Distaplia stylifera Brewin, 1953, p. 60, for synonymy and literature.

Records.—Cape Jaubert, W.A. (Hartmeyer 1919); Shark Bay, and near Perth, W.A. (Michaelsen 1930); Triggs I. and Point Peron, W.A.; Triggs I. (Brewin 1953); Port Denison, Qld. (K3 collection, Australian Museum, E. Allen).

Colony.—As previously described.

Zooid.—Both specimens from Western Australia and from Queensland with 20 longitudinal muscle bands on thorax and at least 20 stigmata in each row. Brewin has not recorded the number of stigmata in her specimens from Triggs I.; however, previous descriptions of the species give the number as 9–18 in each row.

Discussion.—From the occurrence of *D. stylifera* on the Queensland coast, it appears that the species is not confined to the west coast (Brewin 1953), but possibly extends from Fremantle northwards and across the north coast to Port Denison in Queensland. If the species has not been introduced into the Australian area from the Red Sea one would expect it to occur down the Malay Peninsula to be consistent with its occurrence in the north of Australia. It is possible therefore that the species has a very much wider distribution than the records at present show.

Distaplia viridis, sp. nov.

Figs. 28–30

Records.—Victor Harbour, Reevesby I. (5 fm, McCoy Expedition), S.A.

Colony.—Many available. Maximum thickness 1 cm, varying from small circular plates to large investing carpets. Test soft, opaque, of a spongy consistency. Zooids in circular systems around a common cloaca, 10 zooids in each system. Preserved specimens with a slightly greenish tinge in formalin.

Zooid.—3 mm long, thorax and abdomen of equal length in mature expanded colonies. Branchial aperture terminal and 6-lobed. Atrial aperture with a tridentate lip. About 20 transverse muscle bands on thorax; longitudinal muscle bands very few, down either side of dorsal line and fanning out over posterior part of abdomen. Four rows of stigmata with 17 stigmata in each row. Parastigmatic vessels present. Neck fairly long. Stomach cylindrical (Fig. 28), smooth externally but internal surface reticulate. A well-developed gastric gland with large rounded reservoir present. Testes lobes in gut loop and on right side of the loop. There are no female organs present; however, in some colonies an embryo is present in the brood pouch. It is more likely therefore that the ovary matures before the testis and then disappears, than that the colonies are dioecious.

Larva (Figs. 29 and 30).—1·5 mm long. One embryo only present at one time in the brood pouch. Embryo well differentiated at an early stage with the 3 anterior suckers surrounded by cup-like extensions of the sucker-bearing anterior stalk. In later embryos these cup-like extensions broken up into ampullae (Fig. 30) with secondary smaller ampullae arising from their base.

Discussion.—This species is distinguished from other Australian members of the genus particularly by the presence of parastigmatic vessels in the branchial sac and by the transverse thoracic muscles. This latter character relates the species to *D. vallii* Herdman, from which it is distinguished by the stomach lining. *D. domuncula* (Hartmeyer) (Hartmeyer 1913; Michaelsen 1924) from South Africa is also related closely to the present species and may even be identical. However, certain characters of *D. domuncula* including the thoracic musculature have not been described, thus preventing the establishment of their true relationship. Hartmeyer's specimens

were apparently dioecious and only male colonies were available. However, the gonads were scarcely developed in his colonies and it is possible that either they were very immature or that the male and female organs are not present together, as seems probable for the present species. Despite these and other similarities it seems unlikely that these geographically isolated species are the same. Many specimens of *D. viridis* have been taken exclusively from South Australia; only 1 colony of *D. domuncula*, from Walker Bay, South Africa, has been recorded (Hartmeyer 1913).

Genus SYCOZOA Lesson

Four rows of stigmata; atrial aperture with languets; 1 common cloacal aperture at the top of each double row of zooids.

Key to Species of Sycozoa

1. Cup-shaped colonies ..... *S. mirabilis* (Oka)
   Sagami Sea (Oka 1913)
   Colonies not cup-shaped 2
2(1). Both apertures 6-lobed 3
   Both apertures not 6-lobed 4
3(2). Small oval stigmata; weak muscles ..... *S. glauca* Sluiter
   Aru I. (Sluiter 1913)
   Long narrow stigmata; strong muscles ..... *S. sedens* Sluiter
   East Indies (Sluiter 1909)
4(2). Stomach gradually narrows to intestine ..... *S. seizi-wadai* Tokioka
   Arafura Sea (Tokioka 1952)
   Stomach suddenly narrows to intestine 5
5(4). Intestinal gland with rounded reservoir 6
   Intestinal gland without rounded reservoir 7
6(5). Colony folded and pleated ..... *S. cerebriformis* (Quoy & Gaimard)*
   North-west Australia–South Australia–south-east Australia
   Colony not folded and pleated ..... *S. murrayi* (Herdman)*
   South-east Australia, Bass Strait
7(5). Common trunk of intestinal gland same length as stomach ..... *S. quoyi* (Herdman)
   Heard I., Kerguelen (Kott 1954)
   Common trunk of intestinal gland half length of stomach 8
8(7). Head of colony laterally flattened cones ..... *S. tenuicaulis* (Herdman)*
   Victoria, New South Wales
   Head of colony not laterally flattened cone 9
9(8). Colony branched ..... *S. umbellata* Michaelsen
   Patagonia, Tierra del Fuego (Sluiter 1919)
   Colony not branched ..... *S. sigillinoides* Lesson*
   South coast of Australia, New Zealand, sub-Antarctic, Antarctic

S. pulchra (Herdman) (see Sluiter 1913), from Torres Strait, Aru I., and the East Indies, has not been included in the above key owing to lack of distinguishing characters.

Sycozoa murrayi (Herdman)

Fig. 31

Colella murrayi Herdman, 1886, p. 119.
Sycozoa tasmanoides Kott, 1954, p. 157.

Records.—Tasmania (Kott 1954); Bass Strait (Herdman 1886); 10 fm, Bermagui, N.S.W.

Colony.—Five colonies, all fan-shaped, flattened laterally on a fleshy stalk. Largest 5 cm high, of which stalk is 2 cm in length and 1·5 cm in diameter; head 4 cm wide, 1 cm thick. Smallest colony 3·5 cm high, of which stalk is 2 cm in length and 0·8 cm in diameter; head 3 cm wide. Test soft, transparent. Zooids in double rows.

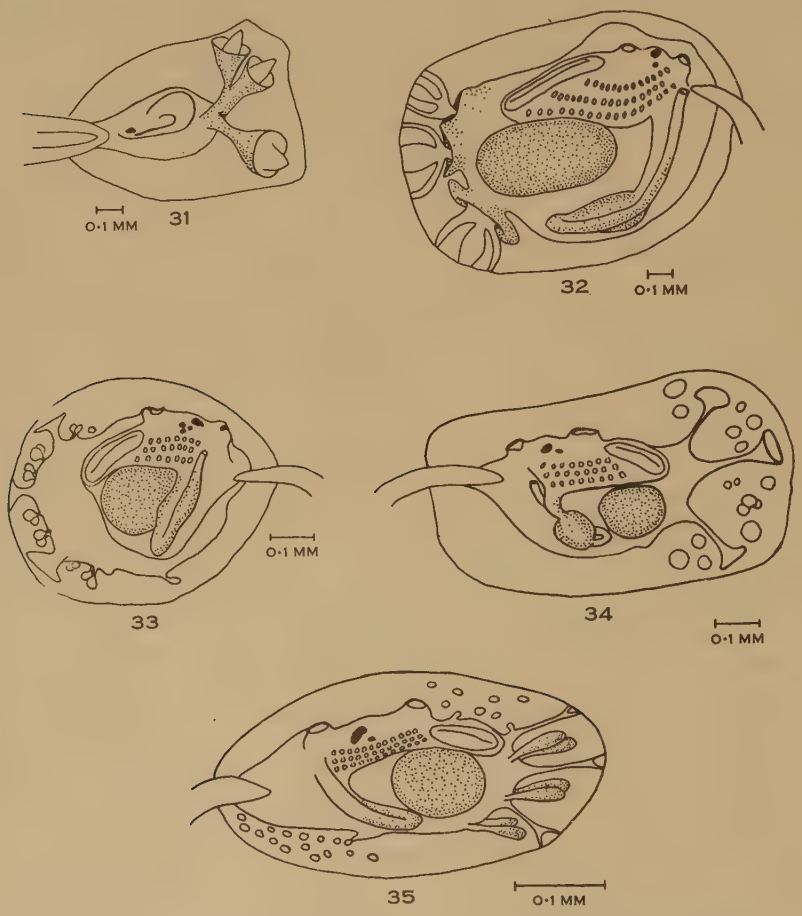

Fig. 31.—*Sycozoa murrayensis.* Ventral view of larva. Fig. 32.—*Pseudodistoma australis.* Larva. Fig. 33.—*Ritterella dispar.* Early larva. Fig. 34.—*R. dispar.* Late larva. Fig. 35.—*Sidneioides tamaramae.* Larva.

Zooid.—Maximum of 2 mm long. In largest colony greater part of double rows along head occupied by brood pouches containing 4 embryos in a single row. Zooids in this colony minute, immature, limited to basal part of head. Zooids from smaller colony mature, with pronounced upper atrial lip, thorax and abdomen of equal length, smooth rounded stomach half way down abdomen. Three testes lobes present in intestinal loop. A small rounded intestinal gland reservoir in gut loop. Colonies of 1 sex only and in these specimens zooids of female or larger colony are regenerating,

the older zooids having disappeared after production of the embryos in the brood pouch.

Larva (Fig. 31).—1 mm long. Three large anterior suckers. Anterior stalk bearing suckers barely developed while stalk of each sucker especially well developed. No ampullae present. Unfortunately, available embryos not in very good state of preservation, and no other details of their form were distinguishable. No precocious budding was observed.

Discussion.—The present colonies agree entirely with Herdman's (1886) description of colonies from south-eastern Australia, although Herdman only had male colonies. The species is characterized by the small zooids and the constant number of 4 embryos in the liberated brood pouch. This latter character is similar to the condition described by Brewin (1953) for *S. tenuicaulis* (see below, *S. tenuicaulis*); however, the larva of the *S. tenuicaulis* exhibits precocious budding which was not observed in *S. murrayi*. The number of testes lobes present in this species is much smaller than those usually found in the genus, and provides a further distinguishing character.

Sycozoa cerebriformis (Quoy & Gaimard)

Aplidie cerebriforme Quoy & Gaimard, 1834, p. 625.
Sycozoa cerebriformis Brewin, 1953, p. 58, for synonymy and literature.

Records.—North-west Australia (Hartmeyer 1919); Victor Harbour and Port Lincoln, S.A.; Balnarring beach, Vic.; Western Port, Vic. (Quoy & Gaimard 1834); South Australia, south-eastern Australia (Caullery 1909); Gunnamatta Bay (mud flats), Jervis Bay, and Port Jackson, N.S.W.

Colony, zooid, and larva.—As described by Brewin (1953).

Sycozoa sigillinoides Lesson

Sycozoa sigillinoides Lesson, 1830, p. 436. Brewin, 1953, p. 56, for synonymy and literature. Kott, 1954, p. 155.

Records.—Fremantle and Garden I., W.A. (Michaelsen 1924); Princess Royal Harbour and Oyster Harbour, Albany, W.A. (Michaelsen 1930); Western Australia (Quoy & Gaimard 1834); Western Port, Vic. (Quoy & Gaimard 1834); D'Entrecasteaux Channel, Tas.; Hobart, Tas.; Bass Strait (Michaelsen 1924).

Colony, zooid, and larva.—As previously described.

Sycozoa tenuicaulis (Herdman)

Colella tenuicaulis Herdman, 1899, p. 64.
Sycozoa tenuicaulis Brewin, 1953, p. 57, for synonymy and literature.

Records.—Lakes Entrance (17–24 fm) and Port Phillip Bay, Vic.; Franklin Sound (Furneaux Group); Jervis Bay and Botany Bay, N.S.W.; Port Jackson and Port Stephens, N.S.W. (Herdman 1899); Port Jackson (Australian Museum collection).

Colony.—Brewin (1953) states that the mature colony contains differentiating zooids in the distal part of the head with 4 embryos in the brood pouch. Several of the colonies in the present collection are completely occupied by liberated brood

pouches with only 1–2 embryos in the brood pouch. Where 2 are present only one is ever in an advanced stage of development. Therefore there must be some variation in the number of larvae which may develop in the brood pouch.

Zooid and larva.—As previously described.

Discussion.—The larvae described by Brewin (1953) were in an advanced stage of development. Therefore it is unlikely that death occurs later to reduce the number of embryos in the brood pouch to the 1–2 which are found in the present colonies. Therefore the number of embryos in the brood pouch cannot be considered a dependable character on which the species may be distinguished. The presence of the precocious buds in the larva does, however, always occur; and the condition of the intestinal gland and the form of the colony are always constant.

IV. Family **POLYCLINIDAE**
Subfamily **EUHERDMANINAE**

There is considerable confusion in this subfamily, owing to the large numbers of monotypic genera which have been defined. As more species in the subfamily are described it becomes apparent that the definition of some of the earlier genera must be expanded in order to cover a wider variation of the characters on which they are based.

Michaelsen (1924) described the genus *Pseudodistoma*, with 3 rows of stigmata and 4 stomach folds. The genus *Ritterella* Harant, with longitudinal stomach folds and 8 rows of stigmata, was established in 1931. Then in 1933 Oka defined the genus *Sigillinaria*, of which the type species, *S. clavata*, has a smooth stomach and more than 4 rows of stigmata. However, *Placentela* Redikorzev, 1914, a genus of the Euherdmaninae with numerous rows of stigmata and a smooth stomach, covers the same range of characters as *Sigillinaria*, and therefore the latter name must be replaced by *Placentela*, which has priority. Since then species with varying combinations of these characters have been described by various authors and assigned to one or other of the above genera. As those species with only 3 rows of stigmata have either a smooth stomach or 4 longitudinal stomach folds, and since the distinction between the stomach with 4 folds and with none at all is often illusive, it is proposed that those species with 3 rows of stigmata form a natural group, and that the genus *Pseudodistoma* should be extended to cover species with a smooth stomach and with 3 rows of stigmata, as well as species with 4 longitudinal stomach folds. The presence of 3 rows of stigmata in the branchial sac is a particularly stable condition in other genera of closely related families, e.g. *Eudistoma*. The definition of *Ritterella* may be conveniently expanded to include species with more than 3 rows of stigmata and with a longitudinally folded stomach. *Placentela* (syn. *Sigillinaria*) may then be limited to those species which, like the type, have a smooth stomach and many rows of stigmata and otherwise generally conform with the original description of the genus. It is considered that the tendency of the zooids to remain free from the common test represents a character of primary importance, and that those colonies with free zooids represent distinct genera from those with embedded zooids. The genera *Dumus* Brewin, 1952, and *Euherdmania* Ritter, 1904, have been defined to receive these species with free zooids.

Larvae, where they are known, are usually of the Polyclininae type or are particularly specialized and therefore at present furnish no further intelligence on the phylogeny of the subfamily.

Genus PSEUDODISTOMA Michaelsen

Zooids embedded; 3 rows of stigmata; stomach smooth or with 4 folds.

Key to Species of Pseudodistoma

1. Stomach with 4 folds 2
   Stomach smooth 3

2(1). With 20 stigmata in each row ..... *P. cereum* Michaelsen
   Stewart I. (Michaelsen 1924)
   With 9–10 stigmata in each row ..... *P. opaca* (Brewin)
   Great Barrier I., New Zealand (Brewin 1950*b*)

3(1). With more than 10 stigmata in each row 4
   With less than 10 stigmata in each row ..... *P. antinboja* Tokioka
   Kii Peninsula (Tokioka 1949)

4(3). Colony with club-shaped lobes ..... *P. novaezelandiae* (Brewin)
   Great Barrier I., New Zealand (Brewin 1950*b*)
   Colony without club-shaped lobes ..... *P. australis*, sp. nov.*
   Rottnest I., W.A.

Pseudodistoma australis, sp. nov.

Fig. 32

Records.—Parrakeet Bay and Rottnest I., W.A.

Colony.—Irregular, investing, not more than 5 mm thick. Test soft, transparent. Zooids scattered throughout, not arranged in systems.

Zooid.—Lying in test at an angle to surface. From 3 mm long in contracted form, 8 mm expanded. Thorax and abdomen of equal length, occupying only 2 mm of length of expanded zooid. Posterior abdomen long. Zooids opening separately to surface by apertures on 6-lobed siphons; branchial aperture terminal, atrial anterodorsal. Twelve longitudinal muscle bands on either side of thorax, continuing as 2 bands along ventral side of abdomen and as 1 wide band along posterior abdomen. Three rows of stigmata with about 25 long narrow stigmata in each row. Oesophagus short; round smooth stomach occupying middle third of abdomen. A well-developed gastric gland present in loop of gut, consisting of branching tubules opening into posterior aspect of stomach. Mid intestine opens into small oval posterior stomach in loop of gut. Junction of oesophagus with stomach extends along most of length of stomach. Gonads present in posterior abdomen.

Larva (Fig. 32).—One developing embryo in brood pouch formed from peribranchial cavity. 1·2 mm long with 3 cup-shaped suckers anteriorly, each surrounded basally by a cup-shaped ampulla.

Discussion.—This species is most closely related to *P. novaezelandiae* (Brewin). The two forms are distinguished by the form of the colony and by a relatively larger stomach in the present species.

Genus RITTERELLA Harant

Zooids embedded; more than 3 rows of stigmata; stomach longitudinally folded.

Key to Species of Ritterella

1. With more than 10 stomach folds 2
   With less than 10 stomach folds 3

2(1). With 5 rows of stigmata ..... *R. dispar*, sp. nov.*
   Queensland
   With 12 rows of stigmata ..... *R. pedunculata* Tokioka
   Sagami Bay, Japan (Tokioka 1953)

3(1). With 4–5 rows of stigmata ..... *R. herdmania*, nom. nov.*
   Green Pools, south-western Australia; Newport and Port Jackson, N.S.W.
   With 8 rows of stigmata ..... *R. aequisiphonalis* (Ritter)
   California (Van Name 1945)

Ritterella dispar, sp. nov.

Figs. 33 and 34

Records.—Caloundra, Qld.

Colony.—Rounded, 1–2 cm in diameter, 8 mm high. Fixed by small area on base of colony. Test soft, transparent. Zooids numerous, vertically placed in test, parallel to one another.

Zooid.—5 mm long; thorax and abdomen of equal length, each 2 mm. Zooids opening separately to surface by terminal 6-lobed branchial aperture and an antero-dorsal atrial aperture with 6 long lobes. Siphons very short. Nine fine longitudinal muscle bands on thorax consisting of only very few fibres. Five rows of stigmata with 16 in each row; length of stigmata becoming progressively less in anterior rows. Oesophagus fairly long; cylindrical stomach present in middle of abdomen. A long duodenal area opens into oval posterior stomach in loop of gut, constricted off from wide rectum occupying ascending loop of gut. About 20 longitudinal folds in stomach wall, occasionally broken up along their length. Gonads present in posterior abdomen, ovary anterior to testis.

Larva (Figs. 33 and 34).—Up to 3 developing embryos present in peribranchial cavity. Well-developed embryo 0·9 mm long. Three suckers with numerous ampullary vesicles free in larval test present anteriorly (Fig. 34). Ampullary vesicles arise in early embryo (Fig. 33) from paired lateral ridges either side of base of suckers. This is similar to the condition found in many larvae of the Polyclinidae. Occasionally there is a multiplicity of the photolith (Fig. 33).

Ritterella herdmania, nom. nov.

Psammaplidium pedunculatum Herdman, 1899, p. 88.
Nec *Ritterella pedunculata* Tokioka, 1953, p. 184.

Records.—Newport and Port Jackson, N.S.W.; Green Pools, W.A.

Colony.—Elongate sandy lobes joined basally. Lobes 3 cm long, 2 mm in diameter, sometimes dividing into two along their length. Test thin and transparent but fairly tough, external test of each lobe thickly encrusted with sand. Colonies from Newport with about 9 zooids in each lobe closely placed around periphery of lobe,

and forming single system with central common cloaca. Specimens from Green Pools smaller, with 4–5 zooids in each lobe. Anterior free end of lobes concave with common cloacal opening in central depression.

Zooid.—Minute, 3–4 mm long. Thorax and abdomen equal in length, together measuring one-third of total length of zooid. Some longitudinal muscles present in thorax, continuing in a band along abdomen. Branchial opening terminal on a short 6-lobed siphon; atrial opening on short 6-lobed siphon, laterally directed and rising from half way down thorax between 2nd and 3rd rows of stigmata. Five rows of stigmata with about 10 stigmata in each row in New South Wales specimens. Specimens from Green Pools with 4 rows of 8 stigmata. Oesophagus moderately long, opening into cylindrical stomach half way down abdomen; stomach wall with 6 distinct folds. A narrow duodenal area, widening into oval posterior stomach; mid intestine expanding into rectum in base of ascending limb of alimentary canal. Gonads present in long posterior abdomen.

Discussion.—The form of the colonies, size of the zooids, and position of the atrial aperture of this species are all distinctive. The species has, in common with *R. dispar* and other related forms, a distinctly folded stomach. Herdman's species in the Australian Museum is identical with the colonies from New South Wales in the present collection.

Genus PLACENTELA Redikorzev

Zooids embedded; more than 3 rows of stigmata; stomach smooth.

There are no specimens of this genus in the present collection, but the following species occur in the areas indicated.

Key to Species of Placentela

Colony arborescent; more than 10 rows of stigmata ..... *P. clavata* (Oka)
Japan (Oka 1933)

Colony consists of flattened lobes on basal membrane; not more than 10 rows of stigmata
..... *P. arenosa* (Brewin)
Great Barrier I., New Zealand (Brewin 1950*b*)

Genus EUHERDMANIA Ritter

Stomach with longitudinal folds; zooids free.

Euherdmania australis, sp. nov.

Records.—Port Phillip heads, Victoria; Camden Haven, N.S.W.

Colony.—An accumulation of sand-covered lobes, joined basally. Lobes 4 cm long. Free anterior end of each lobe flattened, 0·5 cm in diameter, gradually tapering toward the base. Test thin, brittle with sand. Each lobe containing only 1 zooid, opening on flattened upper surface. Openings obscured by sand.

Zooid.—Thorax 0·2 cm, abdomen 0·8 cm in length; long posterior abdomen occupying remainder of length of lobe. In Victorian specimen, the type, branchial opening a transverse slit on edge of flattened upper surface, with dorsal rim

extending to close over ventral rim; atrial aperture in these specimens in centre of lobe. However, in New South Wales specimens the apertures are the usual 6-lobed openings, terminal and anterodorsal respectively, with the branchial opening in centre of upper surface. Twenty simple branchial tentacles of various sizes. Mantle in region of thorax adherent to test; fine longitudinal muscle bands radiating out from siphons, becoming progressively finer toward posterior end of thorax. Twelve rows of 32 elongate stigmata with the ventral 4 reduced in length. Parastigmatic vessels present. Oesophagus short; stomach rounded, its wall with 18 irregular longitudinal folds, sometimes obscure and broken into papillae. An oval posterior stomach before loop of gut. Ovary and testes lobes present in posterior abdomen.

Discussion.—The present species differs from *Euherdmania claviformis* (Ritter) (Van Name 1945, p. 76) in the short oesophagus, in the number and condition of the stomach folds, and in the presence of parastigmatic vessels in the branchial sac. The form of the colony is, however, exactly similar. The modification of the siphonal border in the specimens from Victoria may be due to the very small size of the zooids and the very heavy sand incrustation on and in the thin test. The presence of parastigmatic vessels in the branchial sac suggests that, despite some evidence to the contrary, the genus does belong in the Euherdmaninae. Parastigmatic vessels do occur elsewhere in the subfamily, while they have not been observed in the Clavelininae nor in the Polycitorinae, the other 2 subfamilies in which it has been suggested that the genus belongs. Parastigmatic vessels occur in the Holozoinae; however, this is separated from the Euherdmaninae by very many primary characters. The short oesophagus allies the species to *Homoedistoma* Redikorzev (Huus 1937), from the Sea of Okhotsk; however, free zooids separate it from that genus.

Subfamily **POLYCLININAE**

Genus SIDNEIOIDES Kesteven

Ovary present in thorax.

Key to Species of Sidneioides

1. Colony many pedunculate lobes ..... *S. tamaramae* Kesteven*
   New South Wales
   Colony entire 2
2. Twelve longitudinal muscle bands on thorax ..... *S. japonense* Redikorzev
   Japan (Tokioka 1953)
   Six longitudinal muscle bands on thorax ..... *S. snamoti* Oka
   Japan (Tokioka 1953)

Sidneioides tamaramae Kesteven

Fig. 35

Sidneioides tamaramae Kesteven, 1909, p. 277.

Records.—Merewether (south of Newcastle), N.S.W.; Tamarama Bay, N.S.W. (Kesteven 1909).

Colony.—As described by Kesteven. Lips of common cloaca project well above flattened surface of the sandy lobes. The "tubes" joining the zooids to the common cloaca, however, were not observed.

Zooid.—About 1 cm long, excluding posterior abdomen. Posterior abdomen egg-shaped, or long and spindle-shaped, joined to abdomen by neck of varying lengths. Branchial aperture 6-lobed. Atrial aperture a simple rounded opening on dorsal surface opposite 2nd row of stigmata. A long lip with pointed or dentate tip from body wall anterior to atrial aperture. It may have been this long lip which Kesteven mistook for the "tubes" entering the common cloaca. Very fine longitudinal muscles in body wall. Fourteen rows of stigmata with 12 stigmata in each row. Ovary present at base of right side of thorax between rectum and vas deferens; the latter making a curve ventrally around the ovary. Many testes lobes present in posterior abdomen. Atrial cavity occasionally packed with larvae.

Larva (Fig. 35).—Very small, 0·4 mm long. Three anterior suckers with paired ampullae between and dorsal and ventral to these. Ampullary vesicles above endostyle, arising from dorsal extension of paired germinal ridges. Further ampullary vesicles posteroventrally from posteroventral extensions of these ridges. Form of larva exactly similar to those of other described species of this genus from Japan (Tokioka 1953), and is most closely related to the larvae of *Polyclinum aurantium* Milne Edwards (Carlisle 1952) and *Synoicium pyriforme* (Herdman) (Kott 1954). In this type of larva the lateral ampullary ridges give rise to ampullary vesicles in the posterior ventral and anterodorsal limits, but paired ampullae are retained in the region of the suckers. Median ampullae are not present.

Discussion.—The form of the larvae and zooids are particularly constant in this genus, in which the species are mainly distinguished by the colony. The genus is closely allied to the genus *Polyclinum*.

V. Geographical Distribution

Geographical distribution of species recorded from the Australian coast is set out below. Limits in distribution suggest that these may be defined by geographical areas already described (Kott 1952*a*). Species marked with an asterisk have been taken from one locality only and may have a more restricted distribution within the area. The large number of species recorded exclusively from Rottnest I., W.A., may be due to the intensive collecting on the undercut of the limestone reefs typical of the area. Here many delicate species flourish. No environment providing such protection nor yielding so many species has yet been located in other areas.

Baudinian Region

Sigillina australis Savigny: south-western Australia
* *Eudistoma arenosum*, sp. nov.: Rottnest I.
* *Eudistoma globosum*, sp. nov.: Rottnest I.
* *Polycitor longitubis*, sp. nov.: ?
* *Polycitor translucida*, sp. nov.: Fremantle, Point Peron
* *Clavelina diminuta*, sp. nov.: Rottnest I.
* *Podoclavella ostrearium* Michaelsen: Albany
* *Podoclavella dagysa*, sp. nov.: Rottnest I.
* *Pseudodistoma australis*, sp. nov.: Rottnest I.

Flindersian Region

* *Eudistoma fantasiana*, sp. nov.: Reevesby I.
Polycitor gelatinosa, sp. nov.: Rottnest I.; South Australia
Clavelina baudinensis, sp. nov.: Rottnest I., Balnarring beach
Podoclavella cylindrica Quoy & Gaimard: Fremantle, Bass Strait
Sycozoa sigillinoides Lesson: south coast of Australia (also sub-Antarctic and Antarctic)
Distaplia viridis, sp. nov.: Victor Harbour, Reevesby I.

Maugean Region

Polycitor giganteum (Herdman): Balnarring beach–Port Jackson
* *Polycitor subarborensis*, sp. nov.: Brush I., Ulladulla
Sycozoa murrayi (Herdman): western Tasmania–Bass Strait–Bermagui
Sycozoa tenuicaulis (Herdman): Port Phillip Bay–Port Stephens
Distaplia australiensis Brewin: southern Tasmania
Euherdmania australis, sp. nov.: Port Phillip heads, Camden Haven

Oxleyan Region

Eudistoma elongata (Herdman): Gunnamatta Bay–Moreton Bay
* *Eudistoma parvum* Oka: Long Reef (also Japan)
* *Archidistoma parva* (Sluiter): Lake Macquarie (also East Indies)
* *Clavelina claviformis* (Herdman): Port Jackson
* *Ritterella dispar*, sp. nov.: Caloundra
Sidneioides tamaramae Kesteven: Newcastle area

Dampierian Region

Eudistoma angolanum Michaelsen: north-western and south-western Australia (also West Africa)
Eudistoma ovatum (Herdman): north-western Australia, Torres Strait (also South Africa, Red Sea)
Eudistoma renieri (Hartmeyer): Rottnest I. (also South Africa)
Polycitor circes Michaelsen: north-western Australia, Fremantle
Sigillina magalhaensis (Michaelsen): Houtman's Abrolhos–Fremantle (also Seychelles, Red Sea)
Clavelina enormis (Herdman): north-western Australia–Rottnest I. (also Indian Ocean, Red Sea)
Oxycorynia fascicularis (Drasche): north-western Australia (also East Indies, Malaya, Philippines, Japan)

Solanderian Region

Eudistoma deerata (Sluiter): Great Barrier Reef, Torres Strait (also Malaya)

Solanderian and Dampierian Regions

Eudistoma cyanea (Herdman): Aru I., north-western Australia, New South Wales (also East Indies)
Podoclavella moluccensis Sluiter: north-western Australia–Rottnest I., Great Barrier Reef (also East Indies, Malaya)
Podoclavella meridionalis Herdman: north-western Australia, Great Barrier Reef–Port Jackson.
Distaplia stylifera (Kowalevsky): north-western Australia, Queensland (also Red Sea, South Africa, West Indies)

Random Distribution around Australia

Eudistoma pyriforme (Herdman): Great Barrier Reef, South Australia (also Japan)
Sycozoa cerebriforme (Quoy & Gaimard): Western Australia, South Australia, Victoria, eastern Australia
Ritterella herdmania, nom. nov.: Newport, Port Jackson, Green Pools

From the above lists it will be seen that many species in the Dampierian and Solanderian Regions have a distribution in the East Indies and Malayan area, occasionally extending across the Indian Ocean to South Africa or north to the Red Sea. In these areas the genus *Eudistoma* especially flourishes; and in this genus certain characters appear to be commonly present in those species in any one area. Thus species from eastern and southern Africa have a highly differentiated alimentary canal and well-developed muscles (*E. rhodopyge*, *E. kauderni*, *E. modestum*, *E. renieri*, *E. angolanus*, *E. ovatum*); while species from Malaya and the East Indies are all closely related and show little differentiation of the alimentary canal and no highly developed thoracic musculature (Sluiter 1909). Species from the Pacific area and Japan generally have well-developed alimentary canals but not especially well-developed muscles (*E. parvum*, *E. amplus*, etc.).

The genus *Polycitor* flourishes in Australia generally with many species of limited distribution. Clavelininae are especially numerous in the Baudinian and Flindersian Regions, and Holozoinae flourish in the Maugean Region. It is of interest that the Clavelininae, an apparently primitive subfamily, should be so well represented in the Baudinian Region, since the terrestrial fauna of this area is in some cases considered an ancient fauna (Nicholls 1933).

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THE CULTIVATION OF THE MOTHER-OF-PEARL OYSTER IN THE RED SEA

By The Late C. Crossland*

[*Manuscript received November* 23, 1956]

Summary

This is an abbreviated form of the original manuscript prepared by the author following 16 years' work at Dongonab Bay in the Red Sea in an attempt to establish a pearl oyster cultivation industry.

The environmental conditions at Dongonab, the species of pearl oysters in the Red Sea, and the detailed biology of *Pinctada margaritifera* (L.), the species used for the experiments, are discussed.

Details are given of the methods developed for the collection of spat and the cultivation of the pearl-shell to marketable size. It was unfortunate that the improvements designed in 1921 were not used for commercial production, because the Sudan Government did not continue the scheme.

I. Introduction

Acting under the direction of Professor W. A. Herdman the author spent 5 months, from January to May 1905, in a preliminary survey of the Red Sea pearl fishery, about which practically nothing was known. The resulting report stressed that:

(1) The fishery differs from the well-known Ceylon fishery in that there are no such things as "beds" of oysters in the Red Sea, the oysters occurring in a scattered distribution.

(2) Though the oyster is found almost everywhere there are two specially productive areas, Dongonab Bay and Shubuk Suakin (Fig. 1).

(3) Supervision of the native fishermen would multiply the yield several times.

(4) Some understanding of the factors limiting the numbers of oysters was obtained.

Of these the most important discovery was that of Dongonab Bay, which was peculiarly adapted by nature for experiments on oyster culture and which was subsequently chosen as the site for that purpose (Crossland 1911*a*).

* The late Cyril Crossland was employed from 1905 to 1922 by the Sudan Government to found an industry to cultivate the pearl oyster of the Red Sea. He finally solved the problem of collecting spat and rearing them to marketable size on a commercial scale but at this juncture the price of pearl-shell fell drastically and the Sudan Government did not proceed with the venture. Crossland prepared a manuscript of his work, of which this is a revised and abbreviated edition. The original manuscript, which contains much technical detail, is available in the library of the British Museum.

The manuscript was revised by Mr. J. S. Hynd of the Division of Fisheries and Oceanography, C.S.I.R.O., Cronulla, N.S.W.

The present names of the predator species referred to in Section IV(*e*) are given in a footnote, but no attempt has been made to correct the generic names mentioned elsewhere in the paper.

On Professor Herdman's advice the author was retained by the Sudan Government to supervise the fishery and to experiment with artificial cultivation. It was found that supervision of the native fishery was impracticable owing to the nomadic habits of the fishermen, most of whom were not subjects of the Sudan. Consequently culture studies became the author's main responsibility and Dongonab Bay was closed to fishing to permit experimentation.

Spat collection on a commercial scale was not understood until 1911, and the first large crop was collected in 1912. The handling of a big crop (3 million) by previously established methods was found to be difficult. The consequence was a heavy mortality among the young oysters and stunting of the survivors. It was found that this heavy mortality was avoidable, and under new arrangements it did not recur in the 1914 crop. A period of restricted output from 1914 to 1920 followed. In spite of all the difficulties caused by the war great advances in methods were made, so that as soon as conditions began to approach normal the author was in a position to re-start work on a full scale. The experience of those years of restricted production showed that the oyster could be collected as spat and cultivated to a marketable size with as much regularity as any field crop. Plate 1 shows part of one day's catch drying at Dongonab in August 1922.

In January 1920 a programme was drawn up by which the author bound himself to produce regular annual crops of 4 million, of which 1,660,000 were to attain a fishable size. Cost of materials and labour, interest on capital, etc. were all worked out and given an all-round net price of £80 (stg.) a ton for the shell (the price at the time was over £100 stg.). This would have yielded a satisfactory income even on a capital expenditure swollen beyond all expectation by the war.

In 1920 the whole scheme was held up by the failure of contractors to deliver materials and the greater part of the huge crop of spat collected was thrown away. In 1921, however, when 9 million spat were collected and $4\frac{1}{2}$ million of them accommodated in boxes, the Sudan Government suddenly decided to close the fishery because the price of shell had fallen to £40 (stg.) a ton. Subsequently the market for Red Sea shell did not improve and the culture industry was never revived.

II. Environmental Conditions at Dongonab Bay

The geological structure of Dongonab Bay is peculiar (Crossland 1907*a*, 1907*b*, 1911*a*), providing correspondingly special conditions for marine fauna. In shape Dongonab Bay is like an atoll ring with the added advantage of a tide of only about 1 ft. It is almost completely enclosed by land or reefs. There are large areas of shoal water, with a restricted growth of corals on the western side of the bay. On the eastern side are remarkable rock flats which would support oysters without burying them (Fig. 1).

That conditions were excellent for pearl oysters was indicated by greater numbers of young oysters than elsewhere and also by the heaps of good-sized shell dating from the time when the oysters were taken only for their pearls. Several branches of the bay were found to be too muddy for any quantity of natural collection to take place, and breeding stock was deficient there.

III. Red Sea Pearl Oysters

Of the numerous species and varieties of pearl-shells described by Jameson (1901) three are common in the Red Sea:

(i) *Pinctada margaritifera* var. *erythraensis* (Jameson) (Red Sea mother-of-pearl shell).—This variety is found only in the Red Sea. It was stated by brokers and dealers to differ in quality with the part of the Red Sea it inhabited, specimens from

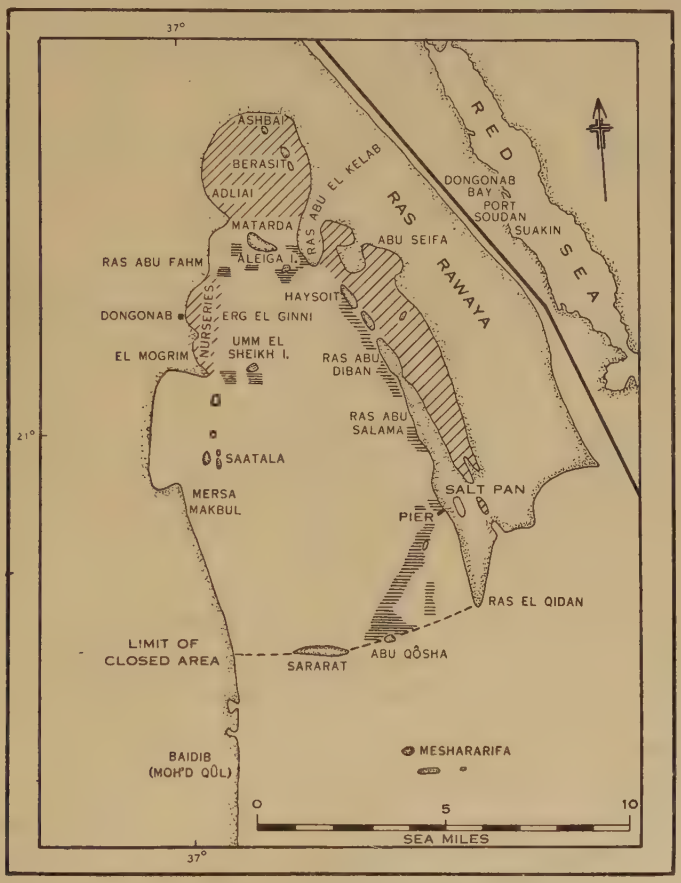

Fig. 1.—Map of Dongonab Bay. Inset, Red Sea.

Areas tried for spat collection.

Areas where oysters were grown on rock bottom.

the south being whiter and therefore more valuable than those from the north. It was the only species taken by the Red Sea fishery and in 1920 a thousand pearl oysters were worth between £10 and £20 (stg.). Few pearls were found; the value of pearls added at most 10 per cent. to that of the shell.

(ii) *Pinctada vulgaris* (Schumacher)* ("Bilbil").—This species is widely distributed, occurring in Ceylon, the Lingah Archipelago, and Japan. It produces

* *P. fucata* (Gould). See Hynd (1955, page 113). (J.S.H.)

pearls but the shells being small and thin are of little commercial value; a thousand pearl oysters of this species in 1920 would have been worth only about five shillings. This species was the most important in the Ceylon pearl fishery, which concentrated on the production of pearls. In Ceylon it occurred in large concentrations in distinct beds and divers brought up large quantities at each dive. However, the fishery in Ceylon was uncertain in its occurrence. It reached a peak about every 10 years. This corresponds with the author's observation of *P. vulgaris* in the Red Sea, where this species was ephemeral and attained sexual maturity and full size rapidly, but was comparatively difficult to cultivate to an age over 2 or 3 years.

(iii) *Pinctada mauritii* (Jameson)* (small "Bilbil").—This is a species of no commercial value. It was described by Jameson (1901, p. 392) from six specimens found on a piece of pumice floating near Mauritius. It is abundant in the Red Sea, and if the author's recollection is correct, large heaps of shells collected in 1901 from the reefs in Zanzibar indicate that natives have searched for pearls in this species.

Spat of all three species of the Red Sea pearl oysters were found on the collectors. The proportion of the two worthless species to the valuable *P. margaritifera* was greatly reduced in later years, partly by the increase in breeding oysters of the latter species, partly by putting out collectors later when the breeding season of the former two species was nearing its end.

The appearance of *P. vulgaris* and *P. mauritii* on collectors in the Red Sea is paralleled by the plague of spat of *P. panasesae* (Jameson), *P. vulgaris*, and *P. sugillata* (Reeve) on collectors in New Guinea and Australian waters (see Jameson 1912).

IV. Biology of P. margaritifera in the Red Sea

(a) *Reproduction*

The sexes are separate and are indistinguishable until the oyster is cut open. Then the sexes can be distinguished even without a microscope as the female product is of a slightly creamy colour and when smeared thinly upon a knife, can be seen to be granular; the male product is apparently homogeneous and white. Under the microscope the female product is seen to be a mass of pear-shaped eggs floating in liquid, like those of *P. vulgaris* described by Herdman (1903). The male product consists of millions of extremely minute spermatozoa.

Oysters begin to breed in the summer of their second year. In the autumn or winter there is no trace of a gonad but about March this develops and fills up all the space in the body cavity. By June the body becomes distended to quite 50 per cent. more than its normal bulk. Discharge of eggs or sperm then occurs at intervals, the gonad decreasing in size until it is again practically invisible in October. *P. vulgaris* on the other hand breeds in winter and spring. The existence of this definite breeding season is important to cultivation, which would be much less successful if eggs and sperm were discharged little by little throughout the year. The eggs are not retained in the gills but are discharged directly into the sea, where they are fertilized.

* *P. maculata* (Gould). Mr. G. L. Wilkins of the British Museum (Natural History) examined Jameson's types of *mauritii* and pronounced them to be identical with *maculata* (Gould). Crossland does not appear to have left any specimens of this species but the original identification appears correct. (J.S.H.)

(b) *Development*

After fertilization, development proceeds while the embryo is floating in the sea. It soon develops swimming and food-collecting cilia and a pair of transparent shells which in a few days are large enough to enclose the embryo. It differs markedly from the adult in the possession of an eyespot, and a long, tongue-like foot for secreting the byssus. At this stage the embryo is with difficulty distinguished from those of other species which are captured with it in the tow-net, but it soon acquires a distinctive form of shell and a slight greenish tinge which distinguishes it from the closely similar larvae of the other two species of *Pinctada*.

The larvae at this stage are just large enough to be seen in a favourable light, appearing like grains of fine sand. The smallest attached spat observed was about the size of a pin's head.

(c) *Setting*

The period of setting is the first and most seriously critical stage, when an enormous mortality occurs. The oyster has to find a suitable substratum to which it can attach itself and begin the manner of life of the adult. The chances of success are remote. Drifting with the currents the majority are carried over deep water. On sinking there the oysters find only fine mud in which they suffocate. The shores of the Red Sea consist of banks of growing coral descending steeply to a bottom of sand or mud. The chances of finding a dead coral branch on which to settle are remote, for the corals themselves are feeding on the plankton of which the oyster larvae are a part. Where stony seaweeds replace the coral the chances are better provided there is enough current to prevent the surface being covered by a film of silt. On the other hand, current and wave motion may be excessive, in which case the young oyster would be rasped to pieces by the moving sand.

However, if the spat makes an unsuitable attachment it may move by means of its active foot. Herdman (1903) observed in Ceylon that great numbers of spat of *P. vulgaris* formed a temporary attachment to certain delicate seaweeds. The same thing is true of this species in the Red Sea but it has not been observed in the young of *P. margaritifera*.

As an energetic search for the attached young of *P. margaritifera* under natural conditions resulted in the discovery of very few specimens smaller than 1 or 2 in. in diameter it must be understood that the foregoing assumes that what was observed under artificial conditions is parallel to the course of nature in the open sea. Enormous numbers of spat were found floating in the sea during June to August but only an infinitesimal proportion of these survived in September. By October it was possible to recognize young *P. margaritifera*.

(d) *Structure and Mode of Growth of the Shell*

A study of the structure of the shell revealed that it is composed of the usual three layers found in molluscan shells: the outer horny layer, the prismatic layer, and the nacreous layer. The shell is produced by the mantle, the extreme outer edge of which secretes the horny and prismatic layers, while the remainder secretes the nacreous layer. The prismatic layer, once laid down, is not added to in thickness.

Further thickening of the shell is possible only by the addition of layers of nacre. Thus instead of the nacre being a mere lining of the shell, as in many bivalves, it forms the bulk of the adult shell. This method of growth by addition to the nacreous layer is of considerable commercial importance to the cultivation of pearl oysters.

Also of commercial importance is the structure of the nacreous layer, which consists of thin plates of calcium carbonate separated by extremely delicate layers of horny material. This alternating layer structure gives a material ideal for buttons and beads because it does not chip nor crack.

The shells of *P. margaritifera* frequently are tinged with yellow at the margins. This part of the shell has to be wasted when the shells are being cut into buttons.

(*e*) *Predators and Parasites*

By October the young *P. margaritifera* are large enough to become the prey of fish, crustaceans, and molluscs.

Several species of fish, particularly *Lethrinus karwa*,* *Chrysophrys bifasciata*, and *Pagrus* sp., were observed to break the shells and eat the oysters up to 18 months old. Larger fish such as *Balistes viridescens* and *B. flavimarginatus* were seen to break up the larger oysters with shells even $\frac{1}{4}$ in. thick. Rays seldom did much damage in Dongonab Bay, though they were able to break up the oyster shells.

Crabs of several species and a hermit crab attacked oysters of up to 4 in. in diameter but their attacks were mainly on the very young stages up to $\frac{1}{2}$ in. diameter.

Murex anguliferus, a gastropod, was the most serious predator. No precautions tried were effective in saving the toll taken in the cultivation areas. The mode of attack by this species has been described (Crossland 1911*b*).

The only internal parasite observed was the larval tapeworm described from *P. vulgaris* by Herdman (1903) and found abundantly in that species in the Red Sea.

Parasites which damaged the shell were a much more serious problem. Five species of boring sponges were found in the mother-of-pearl oyster. The commonest species was red in colour and produced holes 1–2 mm in diameter. A species of *Lithophaga*, a bivalve, was frequently observed boring in cultivated shell. *Polydora* sp., a polychaete worm, was found between the mantle and the shell, where it caused a purplish blister in the nacreous lining of the shell. These parasites were responsible for a 25 per cent. reduction in the value of the marketed crop.

V. Spat Collection

(*a*) *Development of Collection Methods*

It is a well-known fact that for successful collection of spat of a particular molluscan, it is essential to keep down the growth not only of other Mollusca which compete for available food supply but also of all other animals and plants. Collectors must therefore be put into the sea only when breeding of the species required has begun, so that the ground may not be occupied by other organisms.

* The present names of the predators referred to in Section IV(*e*) are as follows: *Lethrinus karwa*=*Lethrinus nebulosus* Forskål; *Chrysophrys bifasciata*=*Acanthopagrus bifasciatus* (Forskål); *Balistes viridescens*=*Balistoides viridescens* (Bloch); *B. flavimarginatus*=*Pseudobalistes flavomarginatus* (Rüppell); *Murex anguliferus*=*Chicoreus anguliferus* (Lamarck).

Eggs and sperm of *Pinctada margaritifera* are ripe in June and are discharged principally in June and July and in decreasing numbers until the middle of September. In 1907, different forms of collector, made of tiles and wood, were sunk in the sea at this period at various points in both shallow and deep water; also all floating objects,

TABLE 1

ANNUAL YIELDS OF THE COLLECTORS, 1908–1921[a]

Year	Number of Collectors	Average Spat per Collector ($\times 10^3$)	Maximum Spat per Collector ($\times 10^3$)	Numbers Cultivated[b] ($\times 10^3$)
1908[c]		40		50
1909[c]		40	99	556
1910[c]	51		9	66
1911[c]	101	Varied greatly	37	413
1912	122	Varied greatly	129	3,000
1913	77	50	97	2,750
1914	42	60	95	1,750
1915[d]	33	20	50	622
1916	50	80	225	3,000
1917[e]	17	41	83	690
1918	17	125	172	1,750
1919[f]	19	200	243	1,500
1920[g]	38	200	Not recorded	772
1921[h]	45	200	421	4,500

[a] From 1908 to 1918 collectors were filled with boards as collecting surfaces. In 1919 boards and bamboos were in use.

[b] This column is not the result of multiplying the average per collector by the number of collectors, as up to 1916 some of the collectors were failures, and these were not counted in making the average. Also in 1916, 1919, 1920, and 1921 large numbers of spat were thrown away owing to lack of cultivation boxes, and these are not included in the totals, which show only the numbers cultivated.

[c] Experimental only.

[d] This is the only year in which a reduced yield was obtained for which the reason remained unknown. Abnormal quantities of an aviculid shell appeared, such as were seen no other year, except on experimental collectors put out at Berasit in the north bay.

[e] Owing to the war causing a shortage, boards of unsuitable quality were used, i.e. of the dom palm, which appeared to contain detrimental substances.

[f] In 1919 the contents of 11 collectors were thrown away.

[g] In 1920 were thrown away the whole contents of 12 collectors, all the spat of ¼-in. size from 23 collectors, and both ¼ in. and ½ in. from 15 collectors. In this year only 23 collectors were put out at the proper time owing to delay in the arrival of materials.

[h] In 1921 the actual contents of the collectors were about 9 millions.

buoys, etc. were carefully observed. In spite of the fact that they were arranged to minimize the effects of sand rasp or fouling by mud, collectors on the bottom were failures in all cases. At most they provided a habitat for one or two specimens of *P. margaritifera*, though large numbers of stony-shelled forms (*Ostrea*, *Chama*, *Spondylus*, *Pecten*) were present. Floating objects were more successful, so that in

1908 a number of larger collectors were devised in which boards were fixed in frames in various positions with regard to light, settling of fine mud, currents, and wave motion. These were anchored afloat on the shoals outside Dongonab harbour, at Ras abu el Kelab, and off Umm el Sheikh Islet (Fig. 1).

Sloping and horizontal boards gave so nearly the same results as vertical that in succeeding years collecting surfaces horizontally arranged were soon abandoned for mechanical reasons. In 1909 more collectors were put out but considerable difficulty was caused by their drifting from their anchorages. In 1910 arrangements were made to collect a large crop but the results were disappointing. Eventually in 1911 it became clear that the reason for their failure was that the collectors (which had been moored closer to Umm el Sheikh Islet to prevent drifting) were within the depth to which sand was stirred up by waves in bad weather. In 1912 the collectors were moored further out and 3 million spat were collected. From that year collection was regular, as seen in Table 1.

(*b*) *Collector Design and Construction*

The collectors used between 1909 and 1921 are illustrated in Plate 1. Essentially a collector consisted of a floating frame 20 ft long by 6 ft wide by 6 ft high, the lower half of which carried the collecting surfaces as a series of vertical shelves 13 ft long by 3 ft wide, the upper part being for the attachment of buoys. In the early experiments these collecting surfaces were deal boards 9 in. by $\frac{1}{2}$ or $\frac{3}{4}$ in., four making up one vertical shelf. Later split bamboos were used in place of the deal boards. The method by which the boards or bamboos were held in place is evident from the photographs. The two lower beams were grooved and a number of short battens, 56 for each collector, $\frac{7}{8}$ in. thick, 3 ft long and 3 or 4 in. broad, slid in these grooves.

Wood in thin boards does not float in the sea for long. At first collectors were ballasted with old tram rails laid in large hooks on the end of the frames. The greatest number of rails practicable would not sink the collectors below the surface until the boards had soaked for a few days. They would then sink until the upper frame was at or near the surface of the water. Until this happened the apparatus was liable to damage whenever the wind rose but when the boards were below the surface it was safe. After about a month the waterlogging of the boards made it necessary to remove the rails one by one, and finally, after about 6 months, not only would all the ballast be removed but the boards became so heavy through waterlogging and the growth of shells etc. upon them that it became necessary to attach sealed 10-gal oil drums as buoys to the upper frames in order to keep the apparatus afloat.

Some difficulty was experienced in mooring collectors owing to the very peculiar sea bottom around the islets and eastern shores of Dongonab Bay. This has already been described in detail (Crossland 1911*a*). This difficulty was overcome by using flat concrete mooring discs 5 ft across and 8 in. thick with a hole in the centre in which the fluke of the anchor fitted.

(*c*) *Principles of Spat Collection*

It was found that successful spat collection was dependent upon a number of factors which are discussed below.

(i) *Locality.*—The localities tested for spat collecting were Ras abu el Kelab, Aleiga Islet, Erg el Ginni shoals, Ras abu Fahm, Berasit, and Umm el Sheikh Islet (Fig. 1), of which the last yielded consistently the best results, with Aleiga second. Ras abu el Kelab and Erg el Ginni were not very successful owing to the proximity of lagoons from which muddy water poured with the falling tide. Collection within the lagoons was a complete failure owing to the fine slimy mud settling upon collecting surfaces. This was fatal to the attachment of spat or to its survival, though a considerable amount of mud appeared to be no detriment to an oyster once it attained a diameter of half an inch or so. Ras abu Fahm was fairly successful, but not nearly so much so as Umm el Sheikh; whereas, as was expected from the character of the surrounding reefs and water, the attempt at Berasit was a complete failure.

The reasons for the superiority of Umm el Sheikh as a collection locality appeared to be the absence of fine mud and the fact that fairly strong currents were directed onto it by a long shoal connecting it to the mainland. These currents were partly tidal, partly wind-driven, and reached 3 kt in heavy storms. They were important in bringing spat to the collectors as well as providing food for subsequent growth. It is probably for this reason that the extreme angle of Umm el Sheikh shoal and the two off-lying shoals generally yielded much better than the parts of the shoal nearer the islet.

(ii) *Depth of Water.*—As far as is known spat setting was unaffected by the depth of water, all other factors being equal. However, in practice the depth in which collectors were moored was restricted to 3–5 fm. In under 3 fm of water there was danger of sand rasp in bad weather; depths over 5 fm were impossible on account of the weight of chain to be supported and the difficulty divers had in placing the anchor fluke in the mooring stone.

(iii) *Weather.*—A heavy storm occurring soon after fixation of the delicate floating spat could remove or cause the death of a large proportion. Consequently the yield was always much greater after a comparatively calm summer. The difference was most strikingly shown on the anchor chains of those collectors which were placed on the shoals away from the islet or on the south-east corner on the main shoal at Umm el Sheikh Islet. Normally the chains and outside portion of the collectors bore no spat at all but after a calm summer the chains of these collectors would be thick with spat, and the angles of the frames would afford sufficient shelter to bear clusters of young oysters. For this reason, and to avoid mechanical troubles, the collectors were not put afloat at the beginning of the breeding season but after the "megili" wind, which blew gales towards the end of June.

(iv) *Date of Putting Out Collectors.*—In the earlier years the mistake was made of putting out the collectors before the breeding season was started. This resulted in the collection of large numbers of *P. vulgaris* and *P. mauritii* and other organisms but few *P. margaritifera.*

(v) *Proportions of Surfaces.*—It was early discovered that an important part of the design was the proportion between the area of each shelf and the distance separating shelves, i.e. the amount of wave motion to which the collecting surfaces were exposed. Should a board shelf 3 ft wide be more than 4 in. from the next, few spat were able to retain their attachment. Should it be under 3 in. almost all were

lost through suffocation. It was generally found that spaces 4 in. wide gave but half the number of spat found in spaces 3 in. wide and that spaces 2 in. wide gave nothing except at the edges.

It was evident from the beginning that fixation was more satisfactory when there were cracks in the boards allowing a passage of water through the collectors. It was impossible to cut the boards into thin strips, because they would have fallen to pieces when attacked by *Teredo* before the time for taking in the collectors. The substitution in 1919 of split bamboos tied into sheets for the shelves instead of boards was tried with excellent results. Not only was the yield increased but the first cost was reduced, and in spite of the vulnerability of a slender stick to *Teredo* a large proportion was used for a second and third year. The sheets were tied with a cheap cord made of dom palm fibre, which was quite rotten by the time the collectors were taken in. Two precautions had to be carefully observed: that no sheet should contain odd splits much thicker than the others, and that the battens should be exactly the right length and thickness and not cut about in filling the frames.

The use of bamboos had the great advantage that ballast could be dispensed with. When placed in the water a bamboo collector floated with the tops of the sheets at water level for 2 days, after which it floated with the buoy frame on the surface. The addition of four buoys was necessary in about a fortnight, to keep the collector afloat until the late summer, when the addition necessary was no greater than that required for board collectors.

Spat settlement depended upon successful penetration of the collector by the larvae and by the food necessary to sustain the young oysters. It was usually found that the front sheet would be thickly covered with well-grown spat, as were to a less extent the four or five next succeeding. In the centre of the collectors the spat decreased in number and most of it in size also.

(vi) *Character of the Collecting Surface.*—It was assumed in the beginning that all boards were suitable for the settling of oysters. However, anomalies in the distribution of spat soon made it clear that slight differences in grain, in roughness of surface, and in resin content all affected results.

Boards which had already been in use and had lost all traces of turpentine etc., or had been roughened by attachment of *Ostrea* and other shells, gave on an average twice the yield that new material did. As, however, more than 25 per cent. of the bamboos were too much broken to be used a second time (even in small frames designed for short pieces) a quantity of new material was necessarily used each year. This was brought into good condition by soaking in the sea for 2 or 3 weeks before use. It was then thoroughly dried, and the animals and plants which had attached themselves to it were killed.

(*d*) *Handling of Spat*

Collectors were raised by bringing them alongside an anchored "sambuk" and one end was hauled a few feet out of the sea by mast tackles (Plate 3, Fig. 1). The wedges at the end of the frame were knocked out, the first pair of battens was slid out, and the top sheet of bamboos removed. As the cord with which it was tied would by this time be rotten the bamboos were passed along loose and piled in the centre of a barge which

was brought alongside. Men sitting on the flat sides of the barge cleared the spat from the bamboos, placing them in perforated 4-gal paraffin tins (see Plate 3, Fig. 2). The bamboos were then piled ashore for the next season.

The tins of spat were taken ashore to a shed near the pier and put through a riddling process (Plate 3, Fig. 3) through three inclined cylindrical rotating sieves, one of 1-in. mesh, the other two of $\frac{1}{2}$-in. mesh wire net.

The spat were thus divided into three sizes, called 1-inch, half-inch, and quarter-inch, after the mesh of the boxes they later occupied in the nursery lagoons. The smallest spat which passed the $\frac{1}{2}$-in. mesh had special treatment in cultivation.

(*e*) *Size Variation in Spat*

Differences in size of the young oysters might be due to differences in age or to retarded growth. The oysters breed from June to September, so that on collectors put out early in July and taken up in November there was spat of all ages between $4\frac{1}{2}$ and $2\frac{1}{2}$ months. Complete records were kept of the numbers of each size of oysters found after riddling through net of 1-in. and $\frac{1}{2}$-in. meshes, and the average size of each set. Also oysters taken from the collectors in October were kept in boxes in lagoons and compared with those taken from collectors in January. The results were surprising, showing that the small size of the majority of the young oysters was not so much the result of their being younger but was mainly due to stunted growth in the collectors. It was found that conditions ideal for fixation of spat were usually quite unsuitable for further growth. In fact, not only were oysters taken from collectors as late as January already stunted, but where taking was delayed, the average yield per collector rapidly decreased, and the oysters which had not migrated to the edges of the sheets had dropped off the boards or bamboos.

The greatly improved growth resulting from removal from the crowded spaces of the collector to boxes in the nursery lagoons is illustrated in Plate 4. Figure 1 shows spat left in a collector until January. Figure 2 shows spat taken from a collector in October and held in $\frac{1}{4}$-in. boxes until January. Repeated experiments to determine whether these smaller oysters eventually grew to the same size as those which reach 1 in. in diameter before they were taken from the collectors indicated conclusively that, after a year's growth, all spat had reached the same size.

(*f*) *New Collector Designs*

In order to avoid heavy initial losses through rough handling and subsequent loss in boxes from attacks by small crabs or smothering, it was desirable that the growth of the oysters should be as rapid as possible while they were on the collectors, and the spat as large as possible when it was placed in the culture boxes. Theoretically the best growth would be obtained by taking in collectors well before the growth of the spat in the narrow spaces of the collectors had caused a shortage of food and oxygen and subsequent stunting, and placing the whole crop in $\frac{1}{4}$-in. boxes from which in 3 or 4 months' time all could be transferred to boxes of 1-in. mesh. This was impracticable because of the cost of the $\frac{1}{4}$-in. boxes, and the heavy loss of small spat under native handling, however well supervised.

In order to secure full growth for the whole crop while still on the collectors, certain modifications of the original design were suggested:

(1) The frames should be of the full 20 ft length but the sheets should be inserted in sets of five, each set separated from the next by a space about 12 in. wide. Each of these frames would therefore carry only about three-quarters of the number of sheets used in the original design, but being widely separated there would be no reduction in the total crop collected and the proportion of well-grown spat would be higher.

(2) For certain areas the frames should be only 10 ft long. The most serious problem here would be the increase in the relative weight of chain to be supported, with the consequent trouble in keeping the apparatus afloat.

(3) In certain areas free from silt and heavy wave action, 4-in. spacing could probably be used safely.

(4) Sheets should be placed longitudinally to allow better penetration of water.

In 1921 a completely different type of collector was designed. A small frame was made from boards and bamboos broken in previous collectors. It was fitted with three pairs of transverse bars connected by a series of vertical bamboo sticks. These were 5 in. apart centre to centre. Flexible split bamboos were then woven onto these uprights in basket fashion. The advantages of this design were:

(1) This collector was more quickly made than that with splits tied to cross-battens.

(2) There was no loss or displacement of bamboos during storms.

(3) The woven sheets were easy to remove in the autumn.

(4) The spat collected grew to a fairly uniform large size and, most important, the numbers caught were comparable with those taken by the original collectors.

This experimental collector was of interest because the bamboos could be removed while the spat was still $\frac{1}{4}$ in. or less in diameter. This was of particular importance to a new method of cultivation worked out in 1922, and discussed in Section VII.

VI. Cultivation

(a) *Cultivation Methods*

When removed from the collectors most of the spat was a little over $\frac{1}{2}$ in. in diameter. For commercial use each shell needed to be 5 or 6 in. in diameter. When $\frac{1}{2}$ in. in diameter the spat was large enough to flourish under conditions that would have been fatal to the microscopic young spat at the time of its fixation in the collectors. It now needed only support above the sand and prevention of overcrowding. The average age of the spat when taken from the collectors was 6 months, and for the next $2\frac{1}{2}$ years it was kept in the nursery lagoons on the west side of Dongonab Bay. It was then transferred to the rocky bottom on the east side of the bay where it remained for 4 years until it was finally fished and sold.

The following account gives the details of the cultivation methods used from 1909 to 1922. While one gang of men was engaged in clearing the spat from a collector, another prepared 100 boxes for the day's crop, placing them along the shore or in shallow water in rows with ballast and covers ready. A certain number of spat was then placed in each division of the boxes (Plate 3, Fig. 4), which were covered carefully and ballast bars arranged, and the whole was then put out in water 3 or 4 ft deep.

A specimen of the boxes used is shown in Plate 5, Figure 1. Each box was 10 ft long exclusive of the legs (which added another 4 in. to each end), 3 ft wide, and 6 in. deep. It was divided transversely into 16 divisions by narrow partitions of $\frac{1}{2}$-in. board, the box itself and the central partition being of $\frac{3}{4}$-in. board. The legs were 18 in. long (so that the bottom of the box was 12 in. above the bottom), and were connected outside the box by a strong bar 1 in. thick by which the whole could be raised or lowered. The bottom of the box was of galvanized wire net, $\frac{1}{4}$-, $\frac{1}{2}$-, or 1-in. mesh, gauge 19, 17, and 14 respectively, and the whole was dipped in hot tar and dried for a week before use. The majority of boxes were tarred annually but those used towards the end of the experiment usually remained in the sea for about 18 months. The tarring was sufficient protection from *Teredo* for the boxes to last, with repair, for years.

The nails used, except for those holding on the net, were galvanized. The ballast used to sink the box consisted of flat bars of cast iron, 3 ft long by 4 in. by 1 in. These were placed at each end over the legs and raising bar. When the box was dry three were required, but later when the box was waterlogged the middle one was removed.

The cover was a length of net of 2-in. mesh, which was sufficient to prevent entrance of the fish *Chrysophrys* and *Lethrinus* and the gastropod *Murex*. In practice a temporary cover of $\frac{1}{2}$-in. mesh was used for the first few days and then replaced with 2-in. mesh. This prevented the spat from being washed out of the boxes by careless handling before they became attached.

In filling the boxes it was found that 20 of the 1-in. size, 30 of the $\frac{1}{2}$-in. size, or 50 of the $\frac{1}{4}$-in. size to each division gave the best results. Each box therefore contained 320 large, 480–500 medium, or 800 small oysters. The boxes were left in shallow water overnight or sometimes for a few days. Care was taken to use only parts of lagoons which were completely sheltered from the prevailing wind, and special precautions were observed should a change of wind appear probable.

With increasing numbers of boxes it became necessary to use the deeper water of the lagoons as well. For conveying boxes to deeper water and raising and lowering them a simple apparatus was devised. It consisted of a rectangular float made of four beams and four sealed drums leaving an open space in the centre 12 by 4 ft, through which a box could be lowered. The orderly arrangement of boxes on the bottom was effected by setting up temporary steel piles at each corner of the area selected and by a system of ropes, guiding the float into any desired position.

The oysters were spread out along the divisions of the box and not allowed to lie in heaps, the cover was carefully replaced, and the box lowered steadily so that

the oysters did not float up through the coarse mesh cover or get washed into corners. In a few days the oysters formed new byssi and were firmly attached to the divisions and to one another. Unfortunately they did not stay as placed but formed clusters, which if left alone resulted in the stunting or death of the innermost. It was therefore necessary to go over the boxes again in 6 weeks' time to break up these clusters into sets of three or four and redistribute them along the divisions in order that all the oysters might get their share of water and food.

By the time this was done the $\frac{1}{4}$-in. spat were mostly large enough to go into the 1-in. boxes, a change rendered desirable by the rapid closure of the $\frac{1}{4}$-in. mesh by mud, weed, and polyzoa, and by the desirability of preserving this very expensive wire. The large oysters were therefore removed from these boxes and put out in those of 1-in. mesh, a change which caused an immediate quickening of growth evidenced by the appearance of new white "fingers" on the edge of the shell. The crowded and therefore stunted oysters were left behind for a while, their chances being greatly improved by the removal of the larger oysters and by the clearing of the net by dashing tins of water upon it. Later in the summer a further set was large enough for removal, and any which had not then attained this size were best thrown away. The boxes were then taken ashore on barges and cleaned and retarred for the next season's work. For economy of time and of boxes the oysters were put out more thickly than they could live when grown up to 3 or 4 in. in diameter. Thinning was therefore necessary for the 1- and $\frac{1}{2}$-in. boxes. The larger oysters were removed and placed in 1-in. boxes at not more than 20 to the division, leaving the same number behind in the original boxes. The oysters were then put out at the rate of 300 to a box, a number which, though appearing as a waste of space at the time, filled the box to overcrowding when most of them attained a size of 3 or 4 in. in diameter.

At this stage of cultivation the most difficult problem was to decide the number of oysters that could be placed in a given area. In most areas the oysters could be placed in the boxes quite thickly provided water could pass through. However, in 1912 when the first large crop of spat was put out, the boxes of 300 specimens put in Mersa Makbul (part of the nursery area, Fig. 1) showed heavy mortality such as was not seen again during the investigation. Dissections of recently dead oysters indicated that food was plentiful so it was concluded that the mortality was caused by poisoning from excreta or lack of oxygen. During the years of the investigation it was found that in certain areas, such as Bay V (northern end of nursery area), many more boxes could be placed than in inshore parts of such enclosed lagoons as Mersa Makbul, and very many more than in El Mogrim (southern end of nursery area).

When the oyster is 3 to 4 in. in diameter, the risk of destruction by fish is inconsiderable. The oyster was at that size transferred to the third stage of cultivation in other lagoons, in which it was placed on trays or "angaribs" (the name of the native bedstead), which allowed a freer circulation of water and economized material, the 2-in. net used in the angaribs being about one-quarter the price of that of 1-in. mesh. These frames were made of bamboo tied by 14-gauge galvanized wire and covered with 14-gauge 2-in. mesh net, the whole dipped into hot tar and dried before use (see Plate 5, Fig. 2). The size was 10 by 3 ft, as for the boxes, but only 200 oysters at the most were placed on this area of 30 sq. ft.

While the oysters remained uncovered they were liable to be pulled off the tray by fish. They were therefore loosely covered with wire net for the first few days until they had anchored themselves to each other, after which they were safe. These angaribs remained for a year without any attention at all, unless a storm disturbed some of them before they had become heavy by waterlogging or before the oysters were fixed to them. Growth at once became more rapid as evidenced by the appearance of new white "fingers" at the edge of the shells. This was due to wider spacing of the oysters, absence of the obstructing sides and divisions of the boxes, and removal from the neighbourhood of the competing organisms growing on the boxes and *Teredo* burrowing in the wood. After a year on these open angaribs the oysters were thrown out onto the flat rock bottoms round the islands and along the east shore of Dongonab Bay, where they remained for 4 years before being finally fished.

(*b*) *Mortality*

Small samples of most of the crops from 1909 to 1918 were kept apart and grown in the harbour; the mortalities of these were recorded. The 1913 sample was still living in 1922 but was the only sample to live so long. All samples showed a negligible mortality up to the sixth year and a 10 per cent. per annum mortality after that. This is taken as the natural mortality rate.

In the full-scale experiments the mortality was very much higher. The following analysis indicates the losses that occurred at each stage of cultivation:

(i) At the time of putting out.

(1) Losses by riddling in the early years were as high as 10 per cent. but the use of more efficient riddles reduced the loss to 1–2 per cent.

(2) Careless handling of boxes with 2-in. mesh covers by unskilled natives resulted in the losses of up to 25 per cent.

(ii) During growth in 16-division boxes.

(1) If a cover were displaced, fish or *Murex* could empty the box in a single night.

(2) Overcrowding brought about by the oysters' own movement resulted in dense clusters and death of some from starvation.

(3) Growth of seaweed sometimes caused suffocation.

The total loss from these three causes was estimated at 25 per cent.

(iii) During the time on open angaribs.

Fish pulled oysters from the frames. Up to 10 per cent. of the crop was lost at this time.

(iv) During the last stage on rock bottoms.

(1) When being placed in these areas some of the oysters fell in shallow holes where they soon died.

(2) Predation by fish and rays took a number of oysters.

The total loss at this stage amounted to 20 per cent. for the 1908–1911 crops and to 30 per cent. of the 1912 crop.

The following losses therefore appear to have been unavoidable:

Starting with		1,000,000 spat
(i) Loss in putting out	5%	300,000
(ii) Loss in 16-division boxes	25%	
		700,000
(iii) Loss during growth in angaribs	10%	70,000
		630,000
(iv) On rock bottoms, say	25%	160,000
Numbers fished		470,000

These figures were obtained by combining results from 1914 onwards for the lagoon stages with those of the earlier crops in the last stage. Lagoon culture improved very greatly after the 1909–1913 crops were handled, but conditions for oysters on the rock bottoms remained the same. The actual results for these early crops, which suffered from the author's lack of experience in those days, were only 25 per cent. of the crop reaching the age of 7–8 years. Besides mortality in the earlier stages, stunting was evident in at least half the crop.

(c) *Rate of Growth*

The samples grown in the harbour referred to above may be taken as indicating the maximum rate of growth. Although individuals of these samples varied widely, the samples themselves were comparatively even in growth.

The results of numerous weighings of the various crops grown on rock bottoms are shown in Figure 2. For comparison the curve is shown for that part of the 1913 crop grown in the harbour. The most obvious feature is the difference between the growth curve for the 1913 harbour sample and the crops grown on rock bottoms. The harbour sample may be taken as the maximum possible growth rate.

Among the curves for the crops on rock bottoms there is a pronounced trend.

The 1908–1910 crops show a conspicuously higher growth rate than the 1912–1914 crops. This is because the 1908–1910 crops were kept on wire longer (and therefore under more favourable conditions) than were the succeeding crops. The 1915 crop shows an improvement on those for 1912–1914. This is due to the fact that in 1915 the collectors bore less spat than previously and the oysters were consequently better grown. Figure 2 shows that growth is most rapid during the first year or two and from that age to 8 or 9 years there is no falling off in the rate of increase of weight. It is especially to be noted that an average weight of 250 g for the shells of each oyster may be expected after $7\frac{1}{2}$ years' growth ($2\frac{1}{2}$–3 years in lagoon nurseries, $4\frac{1}{2}$–5 years on rock bottoms), but that this weight can be attained in $4\frac{1}{2}$ years if the whole life is spent on wire net. This is discussed at length in Section VII.

VII. Future Schemes

From the preceding account of earlier methods it is clear that the last stage of cultivation, in which the oysters were thrown onto the rock bottoms, left much to

be desired. The mortality during this stage was at least 20 per cent. and even up to 40 per cent., and the shells of each oyster weighed only 250 g after 7 years' cultivation. In addition there was considerable damage by parasites, principally *Clione*, which though it had never been observed to cause death, resulted in about half the shells being graded as defectives and therefore less valuable. *Lithophaga* and *Polydora* also contributed to the damage to the shells.

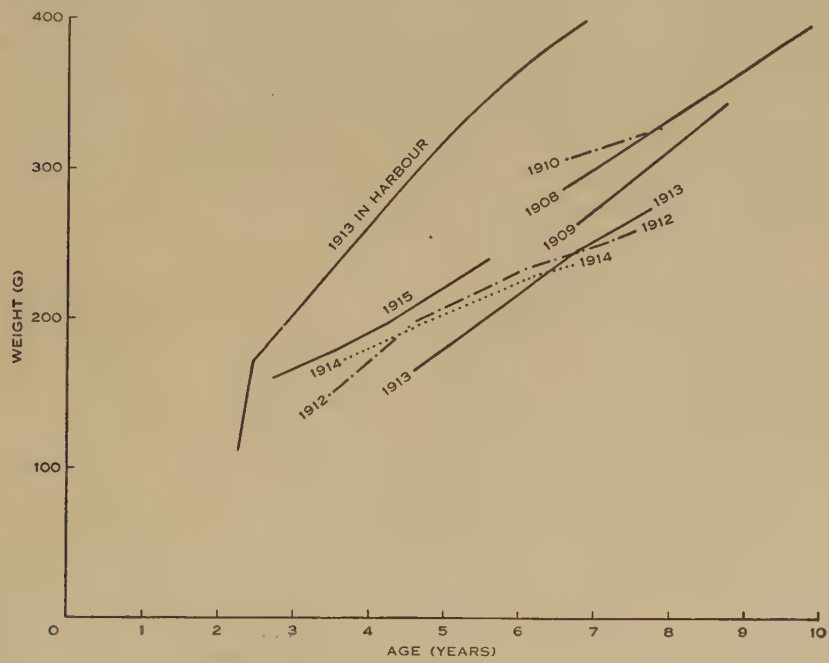

Fig. 2.—Rate of growth of pearl oysters on rock bottoms, Dongonab Bay. The curve for the 1913 special sample kept in the harbour is included for comparison.

It was impossible to reduce the numbers of *Clione* and *Lithophaga* as they were abundant in corals and other organisms. The only solution to the problem of obtaining a larger proportion of perfect shell would have been by:

(i) Fishing the oysters when still young and when parasites were rare if at the same time growth could have been hastened so that a given weight of 250 g could have been attained in a shorter time;

(ii) Keeping the oysters in the lagoons, where *Lithophaga* and *Polydora* were not found.

The proposed new methods would have resulted in the mortality being reduced, probably to about 10 per cent. Shells would have attained the weight of 250 g per pair in 4 to 5 years, thus saving interest on the capital invested, and would have given crops of 80 per cent. sound shell and 15 per cent. very slightly defective. Further, the youngest stage could have been greatly improved. As shown earlier only a small proportion of the spat obtained from the collectors was quite free from stunting, with serious consequences to the cultivation. In the proposed new method

almost all the spat on the collectors could have been grown to the size of the best hitherto obtained, without the use of the expensive $\frac{1}{4}$-in. wire net.

The experiments upon which this scheme was based were as follows. Two ordinary 2-in. angaribs were taken and tray-like covers made of wire 42 in. wide by turning up the sides 3 in. They were filled with pieces of bamboo with $\frac{1}{4}$-in. spat attached, the bamboos being supported by running them through the sides of the cover, which was then turned over onto the angarib. The ends were held down by hooking together the free ends of the net where the meshes had been cut. It was found that this simple arrangement gave complete protection from fish. The angaribs were then placed in the sea until March, when the great increase in size caused the oysters to cover the area of the angarib completely. They were thinned by breaking up the bamboos and spreading the pieces, each with its cluster of young oysters, over four angaribs. Plate 6, Figure 1, shows one of these bamboo splits as taken from a collector in September. Plate 6, Figure 2, shows a similar split grown as described above.

In March the shells were so well grown that net of 2-in. mesh could be used for these clusters. This thinning was not done thoroughly, as the bamboos were still too strong to be readily broken across, but some clusters were very neatly thinned by splitting the bamboo. This led to the idea that if collectors were filled with bamboos split into strips not more than $\frac{1}{2}$ in. broad, the spat upon them would be in bands so narrow that all would be in reach of the food-bearing water even when grown up, and thinning by hand would be unnecessary.

The proposed scheme involved lagoon culture of the complete crop from the $\frac{1}{4}$-in. size spat. It was proposed that rolls of tarred 2-in. net would be supported on bamboo stakes (Sudan bamboo is nearly solid) 3 ft long, notched 6 in. from the top to hold the wire. These stakes would be pushed into the sand, one pair every 8 ft. The addition of a ring of nails driven into each stake would prevent the ascent of *Murex*. A covering of 2-in. mesh and side nets 6 in. high would result in a shallow covered box 36 in. wide, 6 in. high and 50 yd long. The bamboo splits would be taken from the collectors when the spat was of $\frac{1}{4}$-in. size and before stunting occurred owing to overcrowding. These bamboo splits would be suspended by wire hooks from the covering net so that fish could not reach them from below. Under these conditions growth would be a maximum.

Experiment showed that the bamboo splits would last until May or June, by which time the shells would be so large that on collapse of the bamboo splits they would not fall through the net. Provided that they did not fall into too-dense clusters there seemed no reason why they should not remain as they fell until of fishable size—a great simplification over earlier cultivation methods.

The covers and side nets would be tied down with light wire which would rust away in 1 year so that the net would be easily removed toward the end of the year, cleaned, tarred, and used again for the next crop. Its cost would thus be shared by four to six crops. The 2-in. bottom net would last 4–5 years, at which time the oysters would be fished.

The resulting shell would be worth a 60 per cent. higher price and, a most important consideration, would bring a return in 4–5 years instead of 7 years. The advantages and disadvantages of this method may be tabulated as follows:

Disadvantages

(1) Additional cost of net.

(2) Cost of diving gear and barges (it would be necessary to employ pump divers in laying the nets).

Advantages

(1) Addition of 60 per cent. to gross receipts.
(2) A more saleable shell, less yellow in colour and less "cuppy" in shape.
(3) Saving of launch fuel and labour in transferring shells across the bay.
(4) Saving of labour in manufacturing and handling boxes and angaribs.
(5) Prevention of *Murex* attacks.
(6) A far lower mortality.

The figures given below for a 4 million crop were derived by calculation from the percentages given above and shell prices in sterling for 1921. They illustrate the advantages of the proposed new method over that originally used.

	Old Scheme	New Scheme
Annual gross revenue	£19,000	£39,000
Annual expenditure	£15,000	£20,600
Profit	£4,000	£18,400
Percentage return	27%	89%

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Explanation of Plates 1–6

Plate 1

Part of one day's collection recovered from cultivation area in Dongonab Bay. When dry, shells are scraped and packed in shed.

Plate 2

Collectors

Fig. 1.—Old type board collector used in 1910.
Fig. 2.—Collector frames and bamboo splits, 1922.
Fig. 3.—A single frame.
Fig. 4.—One end of frame with six sheets of bamboo splits in position.

PLATE 3

Taking in collectors

Fig. 1.—Frame being hauled up by "sambuk" and boards being loaded on barge.
Fig. 2.—Removing spat from boards.
Fig. 3.—Riddling shed with four riddles. The two tins under the trough are for reception of larger and smaller spat.
Fig. 4.—Counting the spat. Each of the small heaps contains 50 spat ready to be placed on frames.

PLATE 4

Fig. 1.—Box used for cultivation in early years.
Fig. 2.—Tray "angarib" using wire netting and split bamboo.

PLATE 5

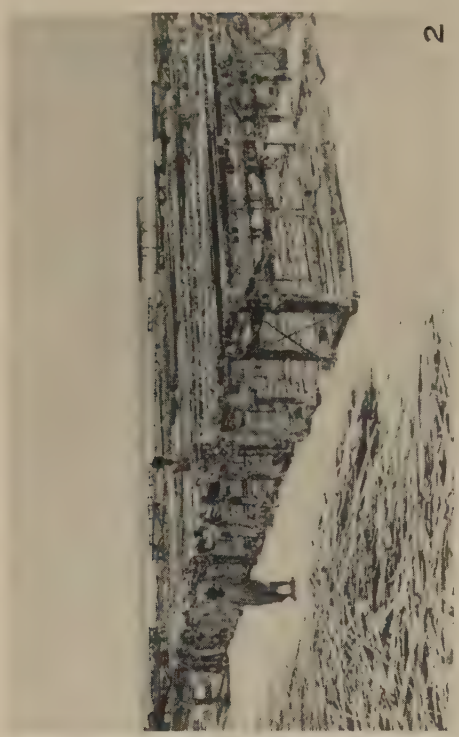
Fig. 1.—Oysters left in a collector until January.
Fig. 2.—Oysters transferred from collector to ¼-in. box in October.

PLATE 6

Fig. 1.—Bamboo split with spat taken from collector in September.
Fig. 2.—Oysters showing quick growth in new type trays.

CULTIVATION OF RED SEA PEARL OYSTER

CULTIVATION OF RED SEA PEARL OYSTER



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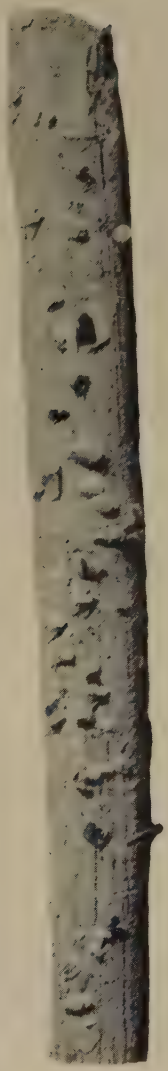

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THE CATABOLISM OF NITROGEN COMPOUNDS IN *DENDROSTOMUM CYMODOCEAE* EDMONDS (SIPUNCULOIDEA)

By S. J. Edmonds*

[*Manuscript received November* 13, 1956]

Summary

The total non-protein nitrogen in the excretory products of fasting specimens of *Dendrostomum cymodoceae* Edmonds was found to be 1·18–1·40 mg N/100 g wet wt./24 hr. Of the total nitrogen, 83–90 per cent. was excreted as ammonia nitrogen, 4–6 per cent. as urea nitrogen, 0–4 per cent. as amino acid nitrogen, and none as uric acid; 89–94 per cent. of the nitrogen was thus accounted for. The results are compared with the corresponding values obtained by other workers for *Sipunculus nudus* and some other invertebrates.

I. Introduction

This paper deals with the end-products of the nitrogen catabolism of the sipunculid *Dendrostomum cymodoceae* Edmonds, 1956. Most of the previous workers on the excretion of sipunculids (Cuenot 1913; Damboviceanu 1926; Delaunay 1926, 1927, 1931; Florkin and Duchateau 1942) used *Sipunculus nudus* and *Golfingia* (*Phascolosoma*) *gouldii* in their experiments. The results with *D. cymodoceae* while in general agreement with those obtained with *Sipunculus* and *Golfingia* differ to some extent from them.

II. Material and General Procedure

Animals, after collection, were kept without food in an aerated aquarium for 4 days. The water was changed daily. During this time the gut became empty so that all the experiments were conducted on fasting animals. Some 15–20 adult animals were carefully washed, weighed, and placed in a flask containing about 200 ml of sea-water (pH 8·0–8·2) slowly aerated at 15–18°C. The air, after bubbling through the sea-water, passed into a small cylinder containing 10 ml of 0·1N sulphuric acid to trap any ammonia which might be expelled by bubbling. After 36 hr the sea-water was run off and the 10 ml of dilute acid added to it. The liquid was then filtered and the filter paper examined for the sparingly soluble uric acid. Any sample found to contain eggs or sperms was discarded. Satisfactory samples were then stored at −5°C and subsequently analyzed for total nitrogen, ammonia nitrogen, urea nitrogen, amino acid nitrogen, and uric acid nitrogen. Controls with sea-water were conducted in each case. Experiments were also carried out to show that dilute solutions of urea, glycine, and uric acid in sea-water are stable for 36 hr when slowly aerated at 18°C. Before estimating the urea and amino acid, 100-ml samples were brought to pH 4 with dilute acid and slowly evaporated over a water-bath to about 20 ml in order to concentrate the solution. Dresel and Moyle (1950) showed that under these conditions solutions of urea and amino acids could be concentrated.

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In order to determine the amount of uric acid present 50-ml samples were evaporated under reduced pressure to about 5–10 ml and tests carried out on this. Solutions containing uric acid can be concentrated under such conditions without decomposition (Dresel and Moyle 1950).

III. Methods

(a) *Total Nitrogen*

Total nitrogen was estimated by the micro-Kjeldahl method. 5-ml samples were heated for 6 hr with 2 ml of concentrated sulphuric acid and the catalyst of Chibnall, Rees, and Williams (1943). After distillation in a Markham still the ammonia was determined colorimetrically with Nessler reagent.

(b) *Ammonia Nitrogen*

Ammonia nitrogen was estimated by the Van Slyke method. A rapid stream of air was passed through 5 ml of sample to which had been added 10 ml of saturated potassium carbonate solution and 2 drops of caprylic alcohol. The ammonia liberated was estimated colorimetrically.

(c) *Urea Nitrogen*

0·1 g of B.D.H. urease was added to 5 ml of a concentrated sample at pH 4–5 and allowed to stand 30 min. Potassium carbonate solution was then added, air blown through the solution, and the ammonia estimated colorimetrically. A control experiment was also conducted with the urease.

(d) *Amino Acid Nitrogen*

Amino acid nitrogen was determined by treating 5 ml of the concentrated sample with ninhydrin at pH 2·5 (Sobel, Hirschman, and Besman 1945). The ammonia formed was removed by aeration and estimated colorimetrically.

(e) *Uric Acid Nitrogen*

Concentrated samples were tested with urea cyanide and arsenophosphotungstic acid according to the method of Buchanan, Block, and Christman (1945). Filter papers used when the original sample was filtered were also examined. No colours developed in either case.

IV. Results

The results of the experiments are shown in Table 1.

V. Discussion

The results of the experiments showed that the total of nitrogenous material excreted by fasting specimens of *D. cymodoceae* when kept in a slowly aerated supply of sea-water was small. Table 2 gives comparative values of the nitrogenous wastes (mg N/10 g/24 hr) excreted by a number of invertebrates. The low rate of excretion of nitrogenous material by *D. cymodoceae*, like its low rate of oxygen consumption

(Edmonds 1957), may be associated with its sedentary habit and its sluggishness. During the experiments the animals showed little or no sign of movement except for occasionally extending and retracting the introvert.

TABLE 1

NATURE AND AMOUNT OF SOLUBLE NITROGENOUS COMPOUNDS EXCRETED BY FASTING SPECIMENS OF D. CYMODOCEAE

The figures in brackets show the percentage partition of the nitrogen in the excreta of the animals

Wt. of Animals (g)	Vol. of Water (ml)	Time (hr)	Nitrogen Excreted (mg/100 g wet wt./24 hr)					Nitrogen Accounted for (%)
			Total	As Ammonia	As Urea	As Amino Acid	As Uric Acid	
180	200	36	1·25	1·07 (86)	0·05 (4)	0·03 (2)	0	92
192	210	37	1·32	1·16 (88)	0·08 (6)	0 (0)	0	94
178	205	34	1·18	1·06 (90)	0·05 (4)	0 (0)	0	94
198	205	36	1·40	1·16 (83)	0·06 (4)	0·03 (2)	0	89
189	200	36	1·21	1·00 (83)	0·05 (4)	0·05 (4)	0	91

The results of the partition experiments, while in accord with the generally accepted view that sipunculids are ammonotelic (Delaunay 1931, p. 292; Prosser *et al.* 1950, p. 191), differed to some extent from those obtained with *Sipunculus* by Delaunay (1931, p. 274), viz. ammonia nitrogen 50 per cent., amino acid nitrogen 16·6 per cent., urea nitrogen 9·7 per cent., purine nitrogen 4·1 per cent., and uric

TABLE 2

THE SOLUBLE NITROGENOUS COMPOUNDS EXCRETED BY SOME INVERTEBRATES

Species	Nitrogen Excreted (mg/10 g wet wt./24 hr)	Author
Dendrostomum cymodoceae (Sipunculoidea)	0·12–0·14	Edmonds (this paper)
Pheretima posthuma (Oligochaeta)	0·52	Bahl 1945
Lumbricus terrestris (Oligochaeta)	0·13–1·13	Cohen and Lewis 1949
Hirudo sp. (Hirundinea)	1·32	Przylecki (quoted by Delaunay (1927, p. 109))
Ascaris lumbricoides (Nematoda)	1·5–2·9	Weinland 1904
Ascaridia galli (Nematoda)	2·9–4·1	Rogers 1952
Marinogammarus marinus (Crustacea)	0·8–1·5	Dresel and Moyle 1950

acid 0 per cent. With *Dendrostomum* the percentage of ammonia nitrogen was higher and that of amino acid nitrogen lower. The results with *D. cymodoceae* approached more nearly those of the two annelids *Aphrodite* sp. (ammonia nitrogen 80 per cent., urea nitrogen 0·2 per cent., and uric acid nitrogen 0·8 per cent.) and

Hirudo sp. (ammonia nitrogen 76·4 per cent., urea nitrogen 5·4 per cent., uric acid nitrogen 0 per cent., and amino acid nitrogen 3·2 per cent.), as set out in Table 24 of Baldwin (1952). Florkin and Duchateau (1942) showed that *Sipunculus* and *Golfingia* possessed a uricase, allantoinase, allantoicase, and urease. This system of enzymes, if present in *Dendrostomum*, could be expected to produce a high percentage of ammonia in the excretory products of the animal.

The presence of small quantities of amino acid nitrogen in the excretory products is not easy to account for. Baldwin (1949, p. 46), attempting to explain the appearance of larger quantities of amino acids in the excretory products of some aquatic invertebrates, suggested: (1) "that the metabolic machinery of the invertebrates may be deficient in some way and incapable of dealing successfully with all the amino-acids derived from the food"; and (2) that the amino acids "may, partly at any rate, simply have leaked out across the body surface". It is possible that either or both of these explanations may hold for *D. cymodoceae* even though the percentage of amino acid nitrogen in the total excretory products is lower. Bahl (1947, p. 136) thought that the protein and amino acid found in the urine of *Pheretima* (Oligochaeta) may have come from the mucus constantly secreted by the animal. *Dendrostomum* like a number of other marine invertebrates secretes mucus. Its body surface is highly glandular and is usually smooth and slippery. Mucus produced by the animal may be the source of some of the amino acid nitrogen found in the excretory products.

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A REVISION OF THE AUSTRALIAN SPECIES OF PENAEINAE (CRUSTACEA DECAPODA: PENAEIDAE)

By W. Dall*

[*Manuscript received November* 26, 1956]

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Summary

Twenty-eight Australian species of Penaeinae, of which six are new, are fully described and figured. Full keys to genera and species, and a glossary of special terms, are included. The zoogeography of Australian and Indo–West Pacific Penaeinae is discussed.

I. Introduction

Although the Penaeidae have long been of commercial importance in other parts of the world, notably in the Gulf of Mexico (Gunter 1950), it is only recently that an appreciable industry has developed in Australia. As a result of commercial and exploratory trawling, several species not recorded in Australian waters or regarded as rare have appeared commonly, the known range of others has been extended, and several new species have been found.

The following 21 species have been described or recorded from Australian waters to date (Hess 1865; Haswell 1879, 1882; Miers 1884; Bate 1888; Whitelegge 1890, 1900; Schmitt 1926; Hale 1927; Racek 1955):

Penaeus maccullochi Schmitt; *P. plebejus* Hess; *P. latisulcatus* Kishinouye; *P. semisulcatus* de Haan; *P. monodon* Fabricius (=*P. carinatus* Dana=*P. caeruleus* Stebbing); *P. esculentus* Haswell; *P. merguiensis* de Man; *P. indicus* Milne Edwards; *P. serratus* Bate (=*Penaeopsis challengeri* de Man); *Penaeopsis novae-guineae* (Haswell); *P. mogiensis* (Rathbun); *Metapenaeus monoceros* (Fabricius); *M. endeavouri* (Schmitt); *M. incisipes* (Bate); *M. mastersii* (Haswell); *M. macleayi* (Haswell); *Trachypeneus curvirostris* (Stimpson); *T. granulosus* (Haswell); *T. anchoralis* (Bate).

To these may be added the following doubtful species which are possibly synonyms: *Penaeus batei* Miers, 1884, Torres Strait (probably a *Metapenaeopsis* sp.); *Penaeus*

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villosus Guerin, "Australia" (in Voy. "Coquille" II and Alcock (1906); quite probably *Metapenaeus monoceros* or *M. mastersii*); *Penaeus gracilis* Dana, Port Jackson (Bate 1888; an immature *Metapenaeopsis* sp.).

The present revision is based on material examined from eastern, northern, and western Australia largely collected since 1949 except for eight uncommon species from the collection of the Australian Museum. Of the species previously recorded, *Penaeus indicus*, "*Penaeus serratus*", and the doubtful species *Penaeus batei*, *P. villosus*, and *P. gracilis*, have not yet been found by the writer. There is every possibility of *P. indicus* being found in numbers on the northern coast of Australia, but *Penaeopsis serratus* is a deep-sea species and is probably rare. *Penaeus maccullochi* is regarded as a malformed *P. plebejus*, and *Metapenaeus incisipes* as a synonym of *M. monoceros*. All holotypes and allotypes and most paratypes have been lodged in the collection of the Australian Museum, Sydney.

II. Morphological Features and Definitions

There are several major works on the Penaeidae, all of which except that of Bate (1888) deal with species outside Australian waters (Alcock 1901, 1905, 1906; de Man 1911; Burkenroad 1934*a*, 1934*b*; Kubo 1949). Kubo's monograph is the most outstanding and comprehensive. An exhaustive comparative account is given of the morphological features of the family, and the systematic part includes full descriptions and keys to subfamilies, genera, and species.

The present revision follows the general scheme of Kubo's (1949) specific descriptions, and for the most part the same terminology is used. Keys include all established Indo–West Pacific species. Order of presentation of genera and species is the same as that in the keys, and does not indicate any supposed phylogenetic relationships (for this see Kubo (1949)).

Features of systematic importance in the Penaeidae are rostrum, carapace, carination of the abdomen, telson, antennules, antennae, mandibles, maxillules, 3rd maxilliped, pereiopods (walking legs), secondary sexual characters (♂ petasma and appendix masculina and ♀ thelycum), and the gastric mill or stomodaeal apparatus (see Kubo (1949) for detailed treatment of these features).

Length and other measurements.—These are made to the nearest millimetre. Total lengths may be approximations owing to the strongly flexed abdomens of some specimens. Length (total length) is taken overall from tip of rostrum to tip of telson with abdomen extended if possible. Carapace length is from postorbital margin to median posterior border. Lengths of other parts are always maximum distances between extreme points unless otherwise noted.

Carapace and rostrum (Fig. 1).—In addition to features shown, some genera possess thin sutures (Fig. 15).

Antennules.—The 1st 3 segments constitute the peduncle. Arising on the lateral base of the 1st segment is the spinous *stylocerite*, and from the median side there is often a foliaceous *prosartema*.

Antennae.—The 1st and 2nd segments are large, the 2nd (*basicerite*) bearing the *scaphocerite* (antennal scale) and 3rd to 5th segments. The 5th (*carpocerite*) carries the long flagellum.

Pereiopods and 3rd maxillipeds.—Lengths of these are measured by extending them along the ventral surface of the body, their extent being referred to suitable prominent morphological features.

Petasma, appendix masculina, and thelycum (Figs. 2–28).—The petasma is always considered as lying parallel to the ventral surface of the body.

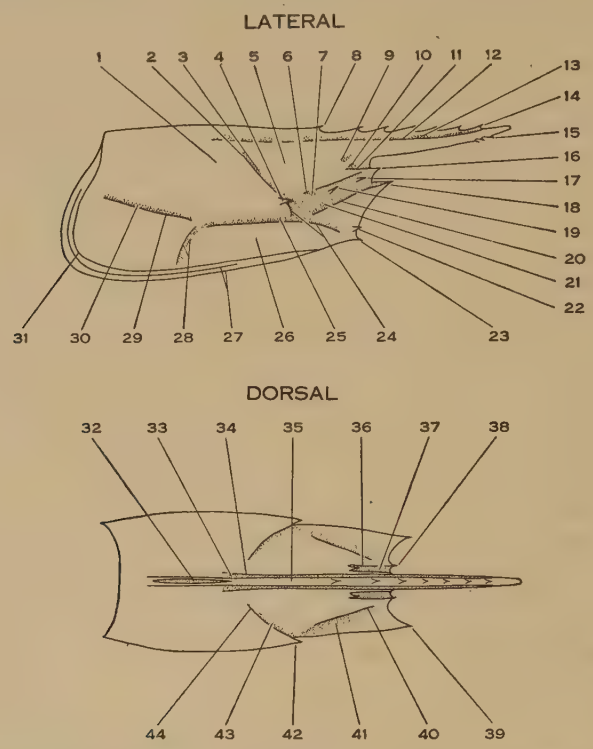

Fig. 1.—Diagrammatic representation of carapace to show features of taxonomic importance.
LATERAL: 1, Cardiac region; 2, cervical carina; 3, cervical sulcus; 4, hepatic spine; 5, gastric region; 6, gastro-orbital carina; 7, orbito-antennal sulcus; 8, epigastric or first rostral tooth; 9, post-ocular sulcus; 10, gastrofrontal sulcus; 11, gastrofrontal carina; 12, adrostral carina; 13, adrostral sulcus; 14, last rostral tooth; 15, last ventral rostral tooth; 16, orbital or supra-orbital spine; 17, postorbital spine; 18, antennal spine; 19, postantennal spine; 20, antennal carina; 21, orbito-antennal sulcus; 22, branchiostegal spine; 23, pterygostomial spine; 24, hepatic carina; 25, hepatic sulcus; 26, pterygostomial region; 27, marginal region; 28, inferior carina and sulcus; 29, branchio-cardiac carina; 30, branchiocardiac sulcus; 31, pterygostomial sulcus.
DORSAL: 32, Postrostral or median sulcus; 33, adrostral sulcus; 34, adrostral carina; 35, postrostral carina; 36, gastrofrontal carina; 37, gastrofrontal sulcus; 38, orbital or supra-orbital spine; 39, antennal spine; 40, gastro-orbital carina; 41, orbito-antennal sulcus; 42, hepatic spine; 43, cervical sulcus; 44, cervical carina.

Gastric mill (Fig. 15).—Use of this as a systematic feature is due to Kubo (1949). Cardiac plate and zygocardiac ossicle are the most useful.

Colour.—The colour in Penaeidae is variable and should not be used alone for specific recognition. However, once the variation is known, in the field, colour and general facies often enable quick identifications to be made. Estuarine juveniles are sometimes differently marked from adults. There is a tendency for prawns from

deeper or more turbid waters to have much darker colours, with red predominating, than those from shallower or clear waters. There is some indication also that colours may vary throughout the geographic range of a species.

Branchiae (gills).—These are of the usual macrurous decapod shape. The rudimentary gills are minute, sometimes microscopic. The *mastigobranchiae* (*epipodites*) are filamentous, long, and often forked.

III. Taxonomy

Family **PENAEIDAE** Bate

Penaeidae Bate, 1888, pp. 220–9. Kubo, 1949, pp. 192–3.

Body compressed, rostrum usually well developed, armed with teeth; eye well developed; antennule with 2 flagella and a stylocerite on 1st peduncular segment; antennal scale very large; mandible with incisor and molar processes not separated by a deep cleft, palp foliaceous 2-segmented; maxillula with 3 laciniae, palp (endopodite) unsegmented or segmented; maxilla foliaceous with 2 laciniae, each typically bifid; 1st maxilliped with a slender endopodite, unsegmented, or 5-segmented; 2nd and 3rd maxillipeds pediform with 7 segments; 1st to 3rd pereiopods chelate, gradually increasing in length backwards; last 2 pereiopods usually with a simple dactylus. Petasma, appendix masculina, and thelycum well developed. Gills numerous, arthrobranchiae in a double series. Ossifications of gastric mill well developed. Cardiac plate with longitudinal row of spinules on inner surface, sometimes without spinules.

Key to the Subfamilies of the Penaeidae

(Non-specialists should consult Barnard (1950) for key to families of the suborder Natantia, which includes the Penaeidae.)

1. Upper antennular flagellum inserted near posterior border of 3rd antennular segment, much shorter than the other, with 7 pleurobranchiae of which all but the last are usually rudimentary; mastigobranch on last thoracic somite ..... Aristaeinae
   Upper antennular flagellum inserted on apex of 3rd antennular segment, equal or subequal to the other; with 2–6 pleurobranchiae all fully functional; no mastigobranch on last thoracic somite 2

2(1). Cervical sulcus reaching to or almost to dorsum; postorbital spine present; mastigobranch on 7th thoracic somite ..... Solenocerinae
   Cervical sulcus reaching not more than $\frac{2}{3}$ distance between hepatic spine and dorsum, often much less; postorbital spine absent; no mastigobranch on 7th thoracic somite .. 3

3(2). Prosartema present; exopods usually present on 2nd and 3rd maxillipeds; pleopods with 2 rami; pleurobranchiae on 4th to 6th thoracic somites ..... Penaeinae
   Prosartema absent; no exopods on 2nd and 3rd maxillipeds; pleopods with 1 ramus only; no pleurobranchiae on 4th to 6th thoracic somites ..... Eusicyoninae

Subfamily **PENAEINAE** Burkenroad

Penaeinae Burkenroad, 1934*b*, p. 72. Kubo, 1949, pp. 260–2.

Rostrum well developed, armed dorsally with teeth, sometimes ventrally armed as well; hepatic and antennal spines usually present; cervical sulcus not reaching dorsum; posterior dorsum of abdomen carinated; telson usually with median dorsal sulcus, tapering to a point, with or without lateral spines. A foliaceous prosartema on inner side of basal segment of antennular peduncle, flagella inserted

on apex of 3rd segment; 2nd segment of mandibular palp lamellar, usually closing a respiratory canal formed by apposition of antennular peduncles and antennal scales; maxillipeds with large endopods; 3rd maxilliped long, pediform, sometimes sexually dimorphic; pereiopods usually not differing greatly in thickness and length, but sometimes last 2 very slender and filiform; exopods usually present on 1st 4 pereiopods. Appendix masculina usually with 2 segments, sometimes with 1 or 3; thelycum with simple open or with closed seminal receptacle. Arthrobranchiae on last thoracic somite usually absent, anterior arthrobranch of penultimate somite usually rudimentary or absent; a podobranch on 2nd maxilliped only; no mastigobranchiae on 7th and 8th thoracic somites.

The subfamily comprises 15 genera: *Miyadiella* Kubo; *Penaeus* Fabricius; *Funchalia* Johnson; *Metapenaeopsis* Bouvier; *Artemesia* Bate; *Parapenaeus* Smith; *Penaeopsis* Bate; *Trachypenaeopsis* Burkenroad; *Macropetasma* Stebbing; *Metapenaeus* Wood-Mason & Alcock; *Protrachypene* Burkenroad; *Xiphopeneus* Smith; *Atyopenaeus* (Alcock); *Trachypenaeus* (Alcock); *Parapenaeopsis* (Alcock). Of these genera *Miyadiella*, *Artemesia*, *Macropetasma*, and *Protrachypene* each contain one species. The genera *Artemesia*, *Protrachypene*, and *Xiphopenaeus* are so far restricted to the Atlantic or Pacific America. Species of the aberrant genus *Miyadiella*, and of *Macropetasma*, *Penaeopsis*, and *Trachypenaeopsis*, which to date are recorded elsewhere in the Indo–West Pacific region, may occur on the northern coasts of Australia. The remaining eight genera are represented in Australian waters: *Penaeus*, *Funchalia*, *Metapenaeopsis*, *Parapenaeus*, *Metapenaeus*, *Atyopenaeus*, *Trachypenaeus*, and *Parapenaeopsis*.

There is a possibility that the International Commission of Zoological Nomenclature may exercise its plenary powers to adjust the spelling of *Atyopeneus* Alcock, *Trachypeneus* Alcock, and *Parapeneopsis* Alcock and other generic names derived from *Peneus* Weber, 1795, to conform with the spelling of the root name *Penaeus* Fabricius, 1798, validated by the Commission in 1955. Pending this decision the spelling *Atyopenaeus*, *Trachypenaeus*, and *Parapenaeopsis* has been adopted in the present revision.

Key to the Genera of Penaeinae

1. A single arthrobranch on 6th and 8th thoracic somites; ophthalmopod greatly elongate, 1st segment of antennular peduncle not excavated for reception of cornea which is as wide as optic peduncle ..... *Miyadiella* Kubo
   An anterior and a posterior arthrobranch on 6th and no arthrobranch on 8th thoracic somite; ophthalmopod not markedly elongate, 1st segment of antennular peduncle excavated for reception of cornea, which is much wider than optic peduncle 2

2(1). A pleurobranch on last thoracic somite; an epipodite on 3rd maxilliped; ventral rostral teeth usually present 3
   No pleurobranch on last thoracic somite; no epipodite on 3rd maxilliped; ventral rostral teeth absent 4

3(2). Incisor process of mandible short, almost right-angled; body glabrous; pterygostomial angle blunt; telson without spines or with 3 pairs of movable spines .. *Penaeus* Fabricius
   Incisor process of mandible elongate, scimitar-like; body densely pubescent; telson with 3 pairs of fixed spines ..... *Funchalia* Johnson

4(2). Petasma symmetrical; 3rd maxilliped usually without basial spine 5
   Petasma asymmetrical; 3rd maxilliped with basial spine .... *Metapenaeopsis* Bouvier

5(4). Telson with a large pair of subapical fixed spines; a spine, which may be minute, on the ventral distomedian border of 1st segment of antennular peduncle 6
Telson without a pair of large subapical fixed spines but often with lateral movable spines (excepting *Parapenaeopsis stylifera* (Milne Edwards)); no spine on the ventral distomedian border of 1st segment of antennular peduncle 9

6(5). Telson with fewer than 4 pairs of fixed spines; basis and ischium of 1st pereiopod each with a spine 7
Telson with 4 pairs of fixed spines; basis and ischium of 1st pereiopod unarmed..... ..... *Artemesia* Bate

7(6). Carapace with longitudinal sutures ..... *Parapenaeus* Smith
Carapace without longitudinal sutures 8

8(7). Branchiostegal spine present; petasma with a pair of large spiniform distolateral projections ..... *Penaeopsis* Bate
Branchiostegal spine absent; petasma with a pair of tubular distolateral projections ..... *Trachypenaeopsis* Burkenroad

9(5). Exopods on 2nd to 4th pereiopods 10
Exopods absent on 2nd to 4th pereiopods ..... *Macropetasma* Stebbing

10(8). A pleurobranch on 7th thoracic somite; no exopod on 5th pereiopod .... *Metapenaeus* Wood-Mason & Alcock
No pleurobranch on 7th thoracic somite; an exopod on 5th pereiopod 11

11(10). Second maxilliped with well-developed exopod; chelae of pereiopods of usual shape .. 12
Second maxilliped without exopod; chelae of pereiopods with short fingers and much-lengthened palm ..... *Protrachypene* Burkenroad

12(11). Dactyls of 4th and 5th pereiopods of usual penaeid shape, not subdivided; usually not more than ½ free portion of rostrum unarmed 13
Dactyls of 4th and 5th pereiopods markedly elongate, filamentous, and subdivided; ⅔ free portion of rostrum unarmed ..... *Xiphopeneus* Smith

13(12). Carapace with longitudinal sutures; thelycum a broad concave anterior plate with rounded anterior margin and transverse posterior plate; ischial spine absent on 2nd pereiopod 14
Carapace without longitudinal sutures; thelycum with narrow anterior plate partly enclosed by 2 raised narrow posterolateral plates; ischial spine on 2nd pereiopod ..... *Atyopenaeus* (Alcock)

14(13). Mastigobranchiae on 3rd pereiopods ..... *Trachypenaeus* (Alcock)
Mastigobranchiae absent on 3rd pereiopods ..... *Parapenaeopsis* (Alcock)

Genus PENAEUS Fabricius

Penaeus Fabricius, 1798. Bate, 1888 (part), p. 229. De Man, 1911, p. 95. Balss, 1914, p. 13. Burkenroad, 1934*b*, p. 74. Kubo, 1949, pp. 268–70. Barnard, 1950, pp. 582–3.

Peneus Alcock 1901, p. 14; 1906, p. 7.

Rostrum toothed ventrally. Carapace without longitudinal or transverse sutures; cervical and orbito-antennal sulci and antennal carinae always present. Hepatic and antennal spines pronounced, pterygostomial angle rounded. Telson with deep sulcus, without fixed subapical spines, with or without lateral movable spines. First antennular segment without a spine on ventral distomedian border. Antennular flagella shorter than carapace. Maxillulary palp with 2 or 3 segments, usually 3. Maxilliped 3 sexually dimorphic. Basial spines on 1st and 2nd pereiopods, exopods on 1st 4 pereiopods, usually present on 5th. Petasma pod-like with thin median lobes, usually with small thickened distal protuberances and forming a posterior tube-like projection; lateral lobes usually with thickened distal rounded margins. Appendix masculina with an ovoid distal segment, bearing numerous

spinules. Thelycum usually with an anterior process, variable in shape, lying between the coxae of 4th pereiopods and seminal receptacle occupying ventral surface of last thoracic sternite, receptacle often closed by 2 flaps which meet or overlap on the mid line; seminal receptacle sometimes open. Zygocardiac ossicle consisting of a principal tooth followed by a longitudinal row of smaller teeth which often end in a cluster of minute teeth. Pleurobranchiae on 3rd to 8th thoracic somites; a rudimentary arthrobranch on 1st, and a posterior arthrobranch on 7th thoracic somites; mastigobranchiae on 1st to 6th thoracic somites. Body glabrous.

Type species *Penaeus monodon* Fabricius (1798) (neotype Holthuis 1949). The genus comprises 28 recognized species of which *Penaeus trisulcatus* Leach, *P. brasiliensis* Latreille, *P. duoarum* Burkenroad, *P. aztecus* Ives, *P. setiferus* Linnaeus, and *P. schmitti* Burkenroad are from the Atlantic (see Anderson and Lindner (1945) for key). The remainder are from the Indo-Pacific. All grow to a large size and most occur in numbers on the continental shelf.

Key to the Indo-Pacific Species of Penaeus

1. Adrostral carina reaching almost to posterior border of carapace; gastrofrontal carina present 2
   Adrostral carina not reaching behind middle of carapace; gastrofrontal carina absent .. 11

2(1). Telson armed, usually with 3 pairs of spinules 3
   Telson unarmed 9

3(2). Postrostral carina sulcate; not more than 1 ventral rostral tooth 4
   Postrostral carina non-sulcate; usually 2 ventral rostral teeth 8

4(3). Sulcus on postrostral carina less than ½ length of carapace; ischial spine on 1st pereiopod. 5
   Sulcus on postrostral carina more than ½ length of carapace; no ischial spine on 1st pereiopod 6

5(4). Seminal receptacle flat, subrectangular; stylocerite reaching ⅔ to ¾ basal segment of antennular peduncle ..... *P. caesius*, sp. nov.
   Seminal receptacle an inverted dome shape; stylocerite reaching tip of basal segment of antennular peduncle ..... *P. longistylus* Kubo

6(4). Rostrum with accessory pair of carinae on blade of rostrum; gastrofrontal sulcus with trifurcate posterior end ..... *P. plebejus* Hess (=*P. maccullochi* Schmitt)
   Rostrum without accessory pair of carinae; gastrofrontal sulcus with bifurcate posterior end 7

7(6). Thelycum with apex of anterior plate rounded; seminal receptacle cylindrical, not closed by 2 flaps; adrostral sulcus narrower than postrostral carina.... *P. japonicus* Bate
   Thelycum with apex of anterior plate bifid; seminal receptacle flat, closed by 2 flaps; adrostral sulcus as wide as postrostral carina ..... *P. latisculcatus* Kishinouye

8(3). Adrostral carinae continuing almost to posterior edge of carapace; anterior plate of thelycum with lanceolate apical process ..... *P. teraoi* Kubo
   Adrostral carinae becoming indistinct posteriorly; anterior plate of thelycum without lanceolate apical process ..... *P. marginatus* Randall

9(2). Rostrum with 1 ventral tooth ..... *P. canaliculatus* Olivier
   Rostrum with more than 1 ventral tooth 10

10(9). Thelycum with a median longitudinal carina on sternite of 7th thoracic somite; ventral surface of flaps of seminal receptacle not pubescent ..... *P. californensis* Holmes
   Thelycum without a median carina on sternite of 7th thoracic somite; ventral surface of flaps of seminal receptacle pubescent ..... *P. brevirostris* Kingsley

11(1). Hepatic carina present 12
   Hepatic carina absent 18

12(11). Third maxilliped in ♂ with apical tuft of setae on propodus; lateral lobe of petasma thickened distally; thelycum with seminal receptacle closed by 2 flaps 13
Third maxilliped in ♂ without apical tuft of setae on propodus; lateral lobe of petasma not thickened distally; thelycum with open seminal receptacle (spp. limited to Pacific America) 16

13(12). Fifth pereiopods with small but distinct exopods 14
Fifth pereiopods without exopods ..... *P. monodon* Fabricius (=*P. carinatus* Dana)

14(13). Postrostral carina sulcate ..... *P. semisulcatus* de Haan
Postrostral carina non-sulcate 15

15(14). Hepatic carina arcuate, extending behind posterior end of antennal carina; rostral teeth 9/2 ..... *P. gracilirostris* Thallwitz
Hepatic carina straight not extending beyond posterior end of antennal carina; rostral teeth 5-7/3-4 ..... *P. esculentus* Haswell

16(12). Adrostral carina reaching as far as epigastric tooth; rostral teeth usually 9/2 ..... *P. vannamei* Boone
Adrostral carina extending posteriorly to epigastric tooth; ventral rostral teeth more than 2 17

17(16). Antennular flagella longer than peduncle; thelycum with prominent pyramidal upheaval on 8th thoracic somite; an expanded coxal projection on 5th pereiopod in ♀ ..... *P. stylirostris* Stimpson
Antennular flagella as long as or shorter than peduncle; thelycum without pyramidal upheaval; no coxal projections on 5th pereiopods of ♀ ..... *P. occidentalis* Streets

18(11). Third pereiopod exceeding scaphocerite by at least dactyl; maxillulary palp 2-segmented 19
Third pereiopod not quite reaching tip of scaphocerite; maxillulary palp 3-segmented ..... *P. orientalis* Kishinouye

19(18). Gastro-orbital carina occupying the posterior $\frac{2}{3}$ distance between hepatic spine and orbital angle ..... *P. indicus* Milne Edwards
Gastro-orbital carina absent or not reaching hepatic spine and occupying the middle $\frac{1}{3}$ distance between hepatic spine and orbital angle 20

20(19). Dactyl of 3rd maxilliped adult ♂ $\frac{1}{2}$ propodus; adrostral carina not reaching as far as epigastric tooth ..... *P. merguiensis* de Man
Dactyl of 3rd maxilliped adult ♂ much longer than propodus; adrostral carina reaching just beyond epigastric tooth ..... *P. penicillatus* Alcock

Penaeus caesius, sp. nov.

Fig. 2*A–G*

Peneus latisulcatus Schmitt 1926, p. 366 (♂ reg. No. E3157, only).

Material.—QUEENSLAND: 12 miles NNE. of Bowen, 19–25 fm (Aust. Mus. regd. No. E3157), holotype ♂ 147 mm, 37 mm carapace; Palm I., Sept. 1952, allotype ♀ 78 mm, 18 mm carapace. LORD HOWE I. (Aust. Mus. regd. No. P5703): paratype ♀ 90 mm, 22·5 mm carapace. WESTERN AUSTRALIA: Lugger Cove, Cygnet Bay (Aust. Mus.), paratypes 3 ♀, 52, 63, 80 mm. *Juveniles.*—QUEENSLAND: Thursday I., 23.x.1949, ♀ 58 mm; Heron I., August 1955, ♀ 56 mm; Aust. Mus. regd. No. P12177, 2 ♀ 31, 43 mm.

Diagnosis

Postrostral carina high, narrow and convex when viewed laterally, postrostral sulcus feeble, $\frac{1}{3}$ length carapace. Stylocerite reaching $\frac{2}{3}$–$\frac{3}{4}$ basal segment of antennular peduncle. Fourth abdominal somite without a dorsal carina. Anterior plate of thelycum spinous anteriorly, seminal receptacle with parallel sides, ventral surface flat, flaps somewhat reflected. With a blue circular patch on 3rd abdominal somite.

Description

Rostrum.—Teeth 10–13/1. Reaching to or almost to tip of antennular peduncle, curving downwards to ventral tooth, distal portion horizontal or slightly upcurved. Fifth tooth usually level with anterior edge of carapace. Postrostral carina feebly sulcate, narrow, and high anteriorly, rostrum having a markedly convex appearance reaching its greatest height at 2nd tooth. Postrostral sulcus $\frac{1}{3}$ length carapace. Adrostral carina ending at $\frac{1}{40}$ length carapace from posterior border, sulcus twice width of postrostral carina.

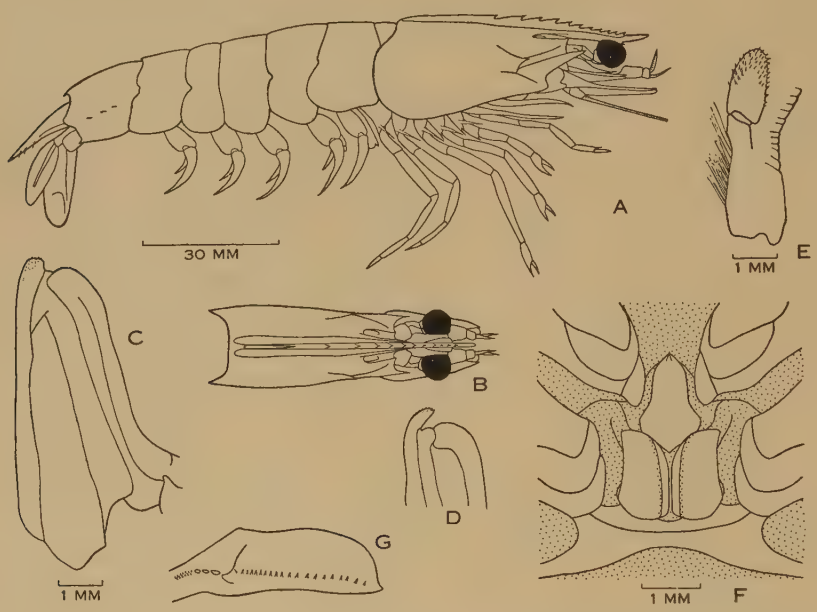

Fig. 2.—*Penaeus caesius*, sp. nov. *A*, holotype; *B*, dorsal cephalothorax; C, inner aspect of left half of petasma; *D*, outer lateral distal portion of petasma (same scale); *E*, appendix masculina; *F*, thelycum of allotype; *G*, cardiac plate and zygocardiac ossicle of allotype.

Carapace.—Gastrofrontal sulcus deep extending to $\frac{1}{5}$ carapace, a bifurcate posterior extremity, small carina causing this bifurcation reaching nearly $\frac{1}{2}$ length sulcus; gastrofrontal carina very high and narrow anteriorly, ending in acute orbital angle. Antennal spine long, reaching about $\frac{1}{2}$ 2nd segment of ophthalmopod. Gastro-orbital carina pronounced, ending at $\frac{4}{5}$ distance between hepatic spine and orbital angle. Antennal carina ending below hepatic spine, orbito-antennal sulcus wide anteriorly and narrowing posteriorly to junction with cervical sulcus at hepatic spine. Cervical sulcus $\frac{1}{5}$ length carapace, ending at $\frac{2}{5}$ length carapace. Hepatic carina sloping downwards with a slight bend at its posterior $\frac{1}{3}$ and ending $\frac{1}{4}$ its length from anterior margin of carapace.

Antennules.—Flagella subequal, $\frac{1}{3}$ length peduncle. Prosartema slightly exceeding, stylocerite attaining $\frac{2}{3}$–$\frac{3}{4}$ basal segment.

Antennae.—Scaphocerite 3 times width, spine slightly exceeding tip of antennular peduncle. Carpocerite almost as wide as long, reaching $\frac{3}{4}$ optic peduncle.

Mandible.—Palp reaching base of carpocerite, distal segment $1\frac{1}{2}$ times width, twice length triangular basal piece. Incisor process with 2 teeth separated by a deep notch, molar process rectangular, posterior corner angular.

Maxillule.—Palp 3-segmented. Basal segment with slightly convex setose inner basal edge, outer edge with rounded protuberance at base bearing a tuft of setae; a curved spine on inner edge with base at $\frac{3}{4}$ segment, a row of about 15 spines on posterior surface. Second segment $\frac{1}{4}$, 3rd $\frac{1}{2}$ length basal segment.

Thoracic appendages.—Third maxilliped not quite reaching tip of 1st segment of antennular peduncle in ♂, reaching as far as or slightly exceeding it in ♀; dactyl ♂ $\frac{3}{4}$ propodus which bears a small apical tuft of setae $\frac{1}{4}$ length dactyl. First pereiopods reaching from base to $\frac{1}{2}$ carpocerite; 2nd exceeding it by dactyl; 3rd reaching from base to $\frac{1}{2}$ 2nd segment of antennular peduncle; 4th and 5th reaching from base to tip of carpocerite. An ischial spine on 1st pereiopod, slightly smaller than basial spine.

Abdomen.—Fourth somite somewhat angular dorsally, but not carinated, deeply incised on posteromedian margin; 5th and 6th somites with a carina, that of 5th ending in a small tooth, that of 6th ending in a larger downcurved spine. Telson armed with 3 pairs of small spines (telson damaged in both holotype and allotype). Sixth abdominal somite with 3 barely perceptible lateral cicatrices.

Gastric mill (Fig. 2*G*).—Cardiac plate with 19-23 spinules. Zygocardiac ossicle a principal tubercle followed by 2-3 smaller blunt tubercles, and an irregular row of 15-28 minute spinous tubercles. Prepyloric ossicle acute, with 9 lateral tubercles and beside these an irregular cluster of very minute tubercles. Cardiac ossicle deeply concave, urocardiac bluntly pointed, pterocardiac tapering and sigmoidal.

Petasma (Fig. 2*C*, *D*).—Reaching most anterior portion of coxae of 5th pereiopods. Median lobes with thickened minutely tuberculate distal protuberances, which exceed the lateral lobes, separated from them by a shallow, smooth depression; but slightly curved ventrally and separated from the lateral lobes when viewed laterally. Median lobes projecting posteriorly beyond lateral lobes by $\frac{1}{5}$ total length of petasma.

Appendix masculina (Fig. 2*E*).—Distal piece 1·5 times as long as wide, symmetrical and oval, the distal $\frac{1}{2}$ anterior surface covered with small setae. Distal piece $\frac{1}{2}$ length basal piece.

Thelycum (Fig. 2*F*).—(Allotype is somewhat immature.) Anterior part of anterior plate with parallel sides and median anterior spine, ventral surface convex; posterior part wide, subpentagonal with concave median depression, angular posteriorly, this angular portion projecting well into seminal receptacle. Seminal receptacle with more or less parallel sides, flaps meeting at mid line, and slightly reflected.

Colour (*freshly preserved allotype*).—Body translucent with narrow blue vertical bands on lower portions of abdominal pleura; circular patch of blue on each side of 3rd abdominal somite, uropods tipped with blue.

Distribution

Lord Howe I.; coast of Queensland; north-western Australia.

Discussion

P. caesius is similar to *P. longistylus* Kubo, from which it may be distinguished by the following features:

Feature	*P. caesius*	*P. longistylus*
Postrostral sulcus	$\frac{1}{3}$ length carapace	$\frac{3}{7}$ length carapace (Kubo 1949, Fig. 109)
Stylocerite	Reaching $\frac{2}{3}$–$\frac{3}{4}$ basal segment of antennular peduncle	Reaching as far as tip of basal segment of antennular peduncle
Second pereiopod	Exceeding carpocerite by dactyl	Exceeding carpocerite by $\frac{1}{2}$ palm
Third pereiopod	Reaching from base to $\frac{1}{2}$ 2nd antennular segment	Reaching tip of antennular peduncle
Cardiac plate	19–23 spinules	28 spinules
Apical projections of median lobes of petasma	Prominent, exceeding the lateral lobes	Not exceeding lateral lobes
Thelycum	Seminal receptacle flat, more or less rectangular, flaps meeting medially, and reflected	Seminal receptacle an inverted dome shape
Circular patch on side of 3rd abdominal somite	Blue	Red
Colour	Translucent with short blue vertical abdominal stripes	Uniformly reddish

The holotype is possibly unusually large for *P. caesius*, as the 78 mm allotype and the 80 mm and 90 mm ♀♀ appear very nearly sexually mature. If ♀♀ of this species are mature at about 100 mm then its smaller size may be a further feature for distinguishing it from *P. longistylus* (Kubo's ♀ is 151 mm). On the other hand, the colour of *P. caesius* may alter with increase in size (cf. *P. plebejus*), penaeids often being more or less reddish in deeper waters. The differences between *P. caesius* and *P. longistylus* are small, and it is possible that a good range of the former would show that the species should be united.

The above 2 species are similar to *P. marginatus* Randall, but the latter possesses 2 or more ventral rostral teeth. *P. caesius* and *P. longistylus* may be distinguished from *P. latisulcatus* Kishinouye and *P. japonicus* Bate by the presence, in the first 2 species, of a high, convex, postrostral carina, and of an ischial spine on the 1st pereiopod.

The adult postrostral sulcation in *P. caesius* is not attained until about 60 mm length (cf. *P. japonicus* (Kubo 1949)). Pereiopods of juveniles are also relatively longer than those of adults.

Penaeus plebejus Hess

King Prawn, eastern Australia

Fig. 3*A–G*

Penaeus plebejus Hess, 1865, p. 168, pl. VII, fig. 19. De Man, 1911, pp. 96, 108–11. Racek, 1955, pp. 223–4.

Peneus plebejus Schmitt, 1926, pp. 367–70.

Penaeus canaliculatus Haswell, 1879; 1882 (not including synonymy). Stead, 1898, p. 209. Whitelegge, 1900, p. 197.

Penaeus canaliculatus var. *australiensis* Bate, 1888, p. 248.

*Peneus macculloch*i Schmitt, 1926, pp. 370–1.

Material.—Noosa River, Qld., to Lakes Entrance, Vic., 12 specimens 40–203 mm; 43 small juveniles and 40 larger prawns, and the Australian Museum collection, have also been examined.

Description

Rostrum.—Teeth 10–11/1, rostrum slightly recurved beyond ventral tooth, reaching not quite or to tip of antennular peduncle. The 5th tooth above anterior edge of carapace. An accessory rostral carina running forward from 1st rostral tooth, extent and distinctness depending on maturity, indistinct in prawns below 50 mm length. Adrostral sulcus as wide as postrostral carina.

Carapace.—Gastrofrontal sulcus deep, extending to $\frac{1}{6}$ carapace, a trifurcate posterior extremity. Orbito-antennal sulcus wide anteriorly, narrowing to junction with the narrow cervical and hepatic sulci. Hepatic carina curving obliquely downwards anteriorly, ending $\frac{1}{6}$ its length from carapace margin.

Antennules.—Outer flagellum longer than inner and $\frac{1}{2}$ length peduncle. Prosartema almost reaching distal end of basal segment; stylocerite attaining more than $\frac{1}{2}$, but not exceeding $\frac{3}{4}$ basal segment.

Thoracic appendages.—Dactyl 3rd maxilliped 0·6–0·7 length propodus, in ♂ bearing an apical tuft of setae $\frac{1}{2}$ length dactyl. Third maxilliped reaching tip of basal segment of antennular peduncle; 1st pereiopod reaching base of carpocerite; 2nd exceeding carpocerite by dactyl; 3rd almost reaching as far as 1st segment of antennular peduncle; 4th and 5th reaching as far as 1st. Ischial spine absent on 1st pereiopod.

Abdomen.—Dorsally carinated from middle of 4th somite, 5th with 1 small lateral, 6th with 3 lateral cicatrices. Telson with 3 pairs of spines.

Gastric mill (Fig. 3*G*).—Cardiac plate with 23–24 spinules; zygocardiac ossicle with principal + 2–3 large teeth and a number of small teeth.

Petasma (Fig. 3*D*, *E*).—Median protuberances projecting very slightly ventrally over distal margins of lateral lobes. (In a 190 mm ♂ these protuberances overhang the distal margins by almost $\frac{1}{3}$ whereas in *P. latisulcatus* they cover $\frac{1}{2}$.)

Appendix masculina (Fig. 3*F*).—Distal piece 1·3 times width, inner edge straight, outer edge convex.

Thelycum (Fig. 3*C*).—A rounded anterior plate lying between coxae of 4th legs and a posterior subrectangular plate, with median groove continuous with anterior piece, fading out posteriorly, flanked by 2 prominent ridges. Flaps of seminal receptacle overlapping medially with outer margins slightly concave.

Colour (*live mature specimens*).—Body cream to yellow; rostrum finely speckled with dark spots, tip banded; postrostral and abdominal carinae dark brown; posterior edge of carapace and abdominal segments light brown; tips of antennal scales and uropods blue, the fringing setae of both bright red; proximal podomeres of pereiopods and pleopods yellow. *Immature prawns*.—Usually cream, sometimes with blue in place of the brown noted above, and short vertical blue bands on pleura of first 4 abdominal somites.

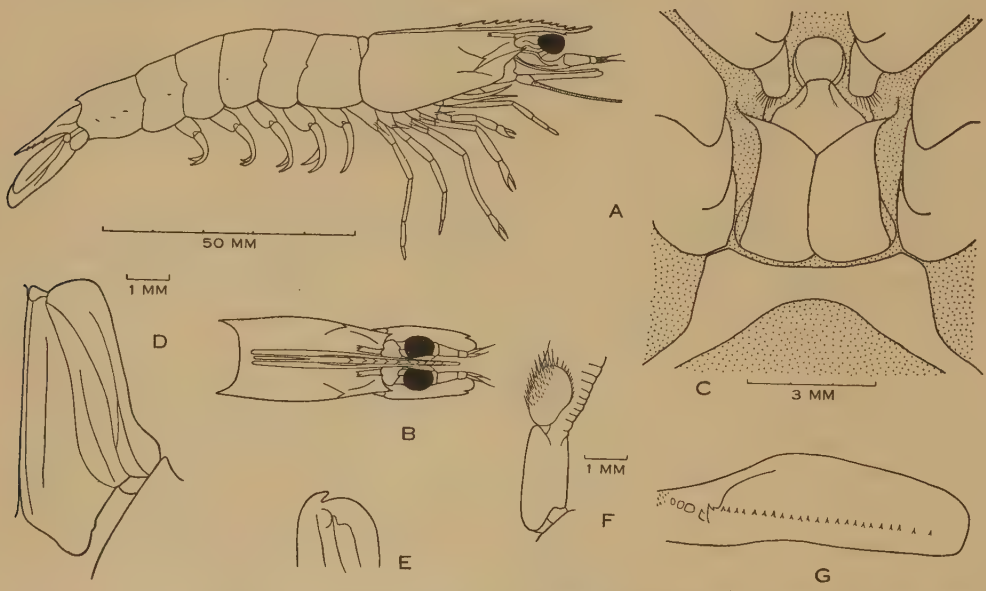

Fig. 3.—*Penaeus plebejus* Hess. *A*, 121 mm ♀; *B*, dorsal cephalothorax of same; *C*, thelycum of 150 mm ♀; *D*, inner aspect of left half of petasma, 125 mm ♂; *E*, outer lateral distal portion of petasma (same scale); *F*, appendix masculina; *G*, cardiac plate and zygocardiac ossicle.

Distribution

East coast of Australia from Lakes Entrance, Vic., to North Reef, Qld. (Schmitt 1926); Auckland, New Zealand (Pesta 1915). Trawled commercially in New South Wales and in south-eastern Queensland though tending to be of irregular occurrence and often associated with *P. esculentus* in the latter region. Juvenile prawns are often found sheltering under rocks at or just below low water spring tide level round Moreton Bay.

Discussion

Kubo (1949) gives features for distinguishing this species from *P. latisculcatus*, but in immature specimens below 5 cm in length the accessory rostral carinae and the small carinae at the posterior end of the gastrofrontal sulcus are not clear, and are thus difficult to distinguish from *P. latisulcatus*. Large specimens of *P. latisulcatus*

have a minute accessory rostral carina, but this carina in *P. plebejus* of comparable size is extensive and well developed. The following additional features for separating the two species are useful:

Feature	*P. plebejus*	*P. latisulcatus*
Rostrum	Reaching not quite to tip of antennular peduncle	Reaching to or beyond tip of antennular peduncle
Postrostral carina	As wide as adrostral grooves	Slightly wider than adrostral grooves
Prosartema	Not quite reaching distal end of basal segment of antennular peduncle	Extending slightly beyond distal end of basal segment of antennular peduncle
Stylocerite	Attaining more than ½ 1st segment of antennular peduncle	Attaining the middle of 1st segment of antennular peduncle
Cardiac plate	23–25 spinules	25–28 spinules
Zygocardiac ossicle	2–3 large tubercles in addition to principal one	3–4 medium-sized tubercles in addition to principal one

Racek (1955) found an immature male of "*Peneus maccullochi*" but states (personal communication) that the X-shaped depression of the postrostral carina as described and figured by Schmitt (1926) was a little different in his specimen, and was in a slightly different place. Since Racek's paper was published he obtained a large specimen with the posterior ½ of the rostrum completely interrupted on the carapace by a smooth break confluent with the adrostral sulci. The rostral blade on either side of this break, which is several millimetres long, is quite smooth. The break has obviously not been freshly made and is the result either of an accident or of a malformation during development. Schmitt (1926) notes that, apart from the interruption of the postrostral carina, there are no features distinguishing *P. maccullochi* from *P. plebejus*. Examination of the holotype of the former by the author confirms this. It therefore seems likely that *P. maccullochi* is a malformed specimen of *P. plebejus*, and is a nomen nudum.

Penaeus latisulcatus Kishinouye

King Prawn, Western Australia

Fig. 4*A–G*

Penaeus latisulcatus Kishinouye, 1900, p. 12. De Man, 1911, pp. 108–11. Kubo, 1949, pp. 278–82. Racek, 1955, pp. 222–3.
Peneus latisulcatus Schmitt, 1926, pp. 365–7 (not incl. ♂ regd. No. E3157).
Penaeus canaliculatus de Man, 1880, p. 185.
Penaeus canaliculatus Oliv. var.? Lanchester, 1901, p. 571.
Penaeus canaliculatus var. *australiensis* de Man, 1902, p. 905.

Material.—WESTERN AUSTRALIA: Cockburn Sound to Warnborough Sound, 20 specimens, 145–193 mm. Australian Museum collection.

Description

Rostrum.—Teeth 8–11/1–2, slightly recurved beyond ventral tooth, reaching tip of antennular peduncle. The 5th tooth just beyond anterior edge of carapace. With a minute accessory carina in specimens above 100 mm, commencing at 2nd tooth and usually becoming indistinct at 3rd tooth. Adrostral carina extending to $\frac{1}{15}$ length carapace from posterior border, the adrostral sulcus slightly wider than postrostral carina.

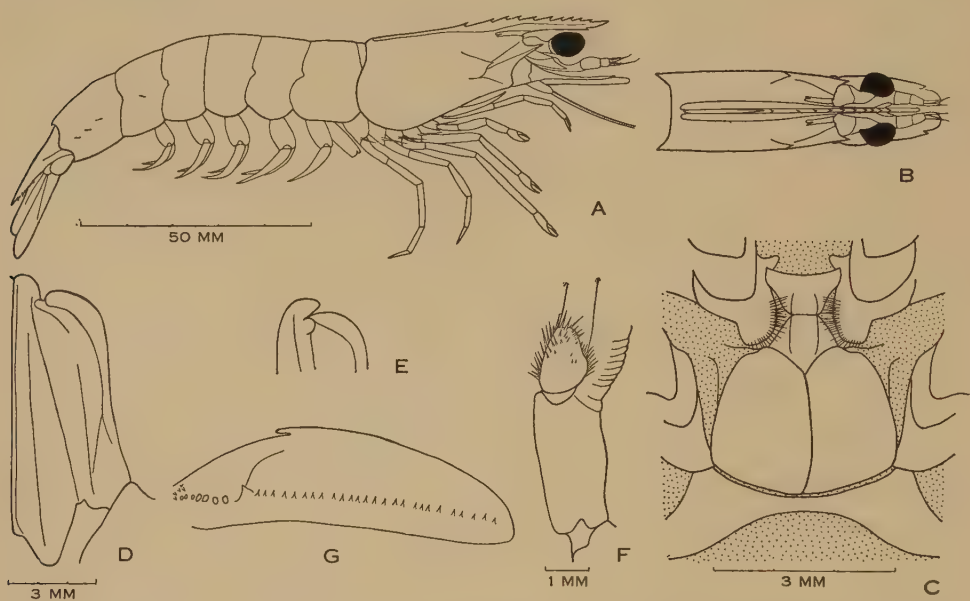

Fig. 4.—*Penaeus latisulcatus* Kishinouye. *A*, 145 mm ♂; *B*, dorsal cephalothorax of same; *C*, thelycum of 189 mm ♀; *D*, inner aspect of left half of petasma, 145 mm ♂; *E*, outer lateral distal portion of petasma (same scale); *F*, appendix masculina, 145 mm ♂; *G*, cardiac plate and zygocardiac ossicle.

Carapace.—Gastrofrontal sulcus deep, extending to $\frac{1}{6}$ carapace, a bifurcate posterior extremity. Orbito-antennal sulcus wide anteriorly, narrowing to junction with the narrow cervical and hepatic sulci. Cervical sulcus extending to $\frac{2}{5}$ length carapace. Hepatic carina curving downwards anteriorly, ending $\frac{1}{6}$ its length from carapace margin.

Antennules.—Outer flagellum longer than inner, and $\frac{1}{2}$ length peduncle. Prosartema reaching distal end, stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Endopod 3rd maxilliped reaching or slightly exceeding tip of 1st segment of antennular peduncle, dactyl 0·7–0·8 length propodus, which bears an apical tuft of setae reaching $\frac{1}{2}$ dactyl in ♂. First pereiopod reaching base of carpocerite, 2nd exceeding it by dactyl; 3rd reaching tip of basal segment of antennu-

lar peduncle, 4th reaching base of carpocerite, exceeding 5th by dactyl. No ischial spine on 1st pereiopod.

Abdomen.—Dorsally carinated from middle 4th somite, carina of 6th ending in a spine, barely curved downwards. Fifth somite with 1, 6th with 3 lateral cicatrices. Telson with 3 pairs spines.

Gastric mill (Fig. 4*G*).—Cardiac plate with 25–28 spinules; zygocardiac ossicle with 3–4 teeth followed by several less distinct teeth and a cluster of minute teeth; prepyloric blunt with 3–4 smaller separated teeth.

Petasma (Fig. 4*D*, *E*).—Median protuberances in lateral view projecting ventrally over distal margins of lateral lobes for $\frac{1}{3}$–$\frac{1}{2}$ thickness of latter.

Appendix masculina (Fig. 4*F*).—Distal piece 1·2–1·3 times width.

Thelycum (Fig. 4*C*).—Anterior plate with median channel, 2 pointed distolateral projections, posterior part subrectangular. Seminal receptacle wider than long, flaps overlapping on mid line, outer margins slightly concave in anterior $\frac{1}{2}$, tending to become convex in large impregnated females.

Colour in life.—Rostrum, postrostrum, edges of scaphocerites, abdominal carina, dark brown; body generally, light yellow to brown; pleura of 1st 5 abdominal somites each with short vertical brown stripe (sometimes blue); antennae light pink; pereiopods light blue to yellow proximally, pink distally; pleopods yellow; uropods yellow to brown tipped with dark blue.

Distribution

Warnborough Sound to Exmouth Gulf, W.A.; Kangaroo I., S.A. (Schmitt 1926); South Australian waters (Hale 1927); Tokyo Bay, Kagoshima, Japan (Kishinouye 1900); Batjan (Molluccas), and Red Sea (de Man 1911); Penang (Lanchester 1901); Korea and Japanese waters (Kubo 1949). Commercially important in Western Australia; recorded from Thursday I. (de Man 1907), and will probably be found scattered down the east coast of Australia.

Discussion

The above description differs from that of Kubo in the following features:

Present Description	Kubo 1949
Third pereiopod reaching distal end of basal segment of antennular peduncle	Third pereiopod reaching tip of 2nd segment of antennular peduncle
Fifth pereiopod shorter than 4th by dactyl	Fifth pereiopod reaching as far as 4th
Appendix masculina distal piece 1·2–1·3 times width	Appendix masculina distal piece 1·6 times width

The Cockburn Sound specimens agree well with the description and Figure 29 of Hale (1927). (See discussion under *P. plebejus* for distinguishing features of *P. latisulcatus*.)

Penaeus monodon Fabricius

Fig. 5*A–E*

Penaeus monodon Fabricius, 1798, p. 408. Holthuis, 1949, pp. 1051–7 (full synonymy *P. monodon* and *P. carinatus*). Kubo, 1949, p. 291 (part synonymy only). Barnard, 1950, p. 584.

Penaeus carinatus Dana, 1852, p. 602, pl. 40, fig. 2. De Man, 1911, p. 101. Racek, 1955, pp. 215–17.

Peneus semisulcatus Alcock, 1906, pp. 10–11.

Penaeus caeruleus Stebbing, 1905, p. 77. Racek, 1955, pp. 217–18.

Penaeus bubulus Kubo, 1949, pp. 296–301.

Material.—Moreton Bay and Townsville, Qld., and Exmouth Gulf, W.A., 9 specimens 100–337 mm. Australian Museum collection.

Description

Rostrum.—7–8/2–3 teeth, usually 7/3; exceeding tip of antennular peduncle, distal ventral tooth at or almost reaching joint between distal and penultimate segments of peduncle. Sigmoidal in shape in juveniles and adults, adrostral carina reaching almost to or to epigastric tooth. Postrostral carina often more or less flat with feeble indications of a sulcus, or sometimes with very shallow sulcus; carina reaching almost to or to posterior edge of carapace.

Carapace.—Length 1·6–1·7 times depth. Gastro-orbital carina occupying posterior $\frac{1}{3}$ to $\frac{1}{2}$ distance between postorbital margin of carapace and hepatic spine. Hepatic carina prominent, anterior $\frac{1}{2}$ horizontal, the posterior often diverging very slightly below horizontal axis; distinctly separated from base of antennal carina, which ends above middle of hepatic carina. Hepatic sulcus ill defined. Cervical sulcus often with upper $\frac{1}{3}$ indistinct, $\frac{1}{5}$–$\frac{1}{7}$ length carapace.

Antennules.—Flagella subequal, equal to, or slightly longer than peduncle. Prosartema reaching to or barely exceeding tip, stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Endopod 3rd maxilliped reaching tip of antennular peduncle in adult ♂, reaching distal end of basal segment of antennular peduncle in ♀ and juvenile ♂. Dactyl almost length propodus in ♂, hollowed, inserted at $\frac{1}{5}$ length propodus from distal end which bears a tuft of setae as long as dactyl. Dactyl $\frac{1}{2}$–$\frac{2}{3}$ length propodus in ♀ and inserted apically. First pereiopod reaching distal end of or slightly exceeding carpocerite, 2nd reaching distal end of basal segment of antennular peduncle, 3rd reaching to or exceeding tip of peduncle by dactyl, 4th reaching as far as 1st, 5th exceeding 4th by dactyl. Ischial spine on 1st pereiopod; no exopod on 5th leg.

Abdomen.—Dorsally carinated from anterior $\frac{1}{3}$ of 4th somite, carina curving downwards fairly strongly towards posterior end of 6th somite. The 4th and 5th somites each with a small cicatrice, 6th with 3 cicatrices. Telson unarmed.

Gastric mill (Fig. 5*E*).—Cardiac plate with 18–24 spinules, usually 20–24; zygocardiac ossicle principal + 9–12 conical teeth, usually 9–10, followed by several smaller teeth and a cluster of minute teeth; prepyloric acute with 6–8 large teeth, sometimes with 2–3 smaller teeth, on lateral margin.

Petasma (Fig. 5*C*).—Median anterior lobe small, separated from lateral by a shallow notch, not projecting as far as lateral lobes. Lateral lobes without distal setae, with distolateral irregular group of ossicles greatly variable in number.

Appendix masculina (Fig. 5*D*).—Length distal piece 1·6–1·7 width; at least basal $\frac{1}{2}$ naked.

Thelycum (Fig. 5*B*).—Length anterior plate twice width, anterior rounded portion concave, posterior bluntly pointed portion inserted between flaps of seminal receptacle for $\frac{2}{5}$ their length. Seminal receptacle circular, flaps forming tumid reflected lips on mid line, with smooth inner edges in impregnated females.

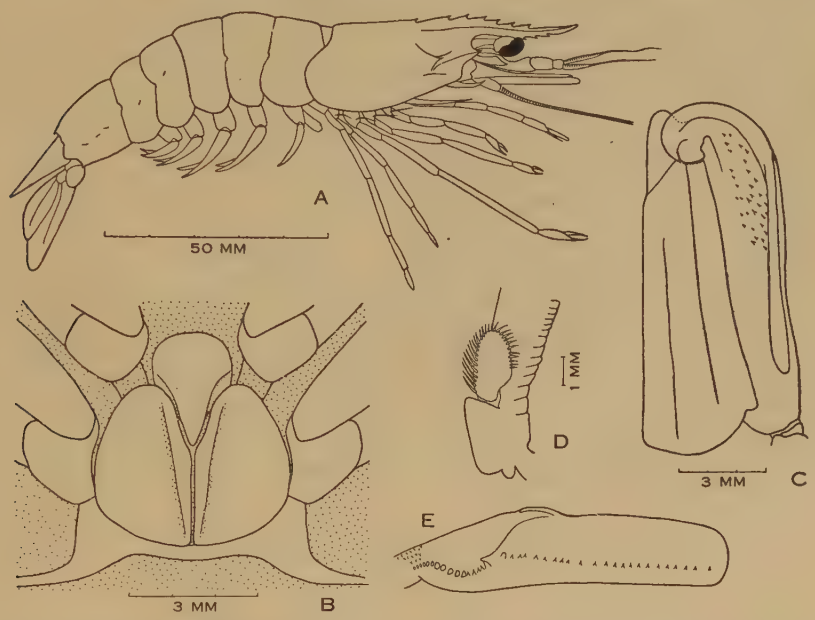

Fig. 5.—*Penaeus monodon* Fabricius. *A*, 140 mm ♂; *B*, thelycum of 227 mm ♀; *C*, inner aspect of petasma, 198 mm ♂; *D*, appendix masculina; *E*, cardiac plate and zygocardiac ossicle.

Colour (*freshly preserved specimens*).—Carapace and abdomen transversely banded, abdomen with 2 to each somite, posterior mid brown, anterior greyish brown. Rest of the body ranging from light brown to blue. Pleopods brown to blue, fringing setae red. A 126 mm ♀ from Goodna, Brisbane River, possessed (freshly preserved) a dull-red dorsal strip, width of body, running from rostrum to 6th abdominal somite, rest of animal an inky blue. Only *Metapenaeus mastersii* normally penetrates the Brisbane River to this distance, so this specimen should be regarded as abnormal. Barnard (1950) gives the general colour as "pale buff, more or less transparent, minutely speckled with blue", except for the *caeruleus* variety which is "vivid blue". Kubo (1949) states that *Penaeus bubulus* resembles the colour of a Japanese ox (usually a light fawn), which roughly accords with Barnard's description. The prawns from Moreton Bay when freshly preserved ranged from vivid blue to predominantly brown, while those from Townsville were more or less buff with little or no blue.

Distribution

Moreton Bay and Townsville, Qld.; Exmouth Gulf, W.A.; East London to St. Lucia Bay, South Africa (Barnard 1950); Karachi to Mergui and the Andamans

(Alcock 1906); Tokyo Bay and Bay of Ise, Japan, Makassar, Atjeh, Singapore (de Man 1911); Yokohama, Formosa, Amoy, Celebes (Kubo 1949). Common commercial prawn of Calcutta (Alcock 1906); uncommon off southern Queensland, occasional specimens appearing in catches of *P. esculentus*, but becoming more common at Townsville.

Discussion

The above description accords with that of Barnard (1950), who states that he has "no hesitation" in making *caeruleus* a synonym; and that he "would not even regard it as a colour variety". The coloration of the Moreton Bay specimens lead the present writer to the same conclusion. There is no apparent difference in lengths of antennular flagella as noted by Anderson and Lindner (1945), and, in addition, the filamentous portions tend to be broken off in large specimens, which could easily lead to an error in this respect.

Alcock (1906) erroneously assigned *P. semisulcatus* to *P. monodon*, which has partly been responsible for confusion between these species, as indicated by Barnard (1950). Kubo (1949) has apparently followed this error, but has created *P. bubulus*, the brief description of which agrees with that of *P. monodon* except for length of 5th pereiopod and armature of the prepyloric ossicle. It is thought best, therefore, to regard *P. bubulus* as a synonym. Holthuis (1949) has shown that *P. carinatus* Dana is identical with *P. monodon* Fabricius, the latter having priority. (See discussion under *P. semisulcatus* for features of difference between the 2 species.)

Penaeus semisulcatus de Haan

Fig. 6*A–E*

Penaeus semisulcatus de Haan, 1850, p. 191, pl. XLVI, fig. 1. De Man, 1911, pp. 97–100. Racek, 1955, pp. 218–19.

Penaeus monodon Bate, 1888, p. 250. Kubo, 1949, pp. 291–6 (including only part synonymy).

Peneus monodon Alcock, 1906, p. 8.

Penaeus ashiaka Kishinouye, 1900, pp. 7–14. Rathbun, 1902, p. 38. Nobili, 1903, p. 2; 1906, p. 16.

Material.—QUEENSLAND: Bowen Harbour (Aust. Mus. regd. Nos. P6024-5), 2 ♂ 119, 131 mm; off Townsville, ♂ 137 mm. NEW GUINEA: Milne Bay, ♀ 190 mm, coll. A. M. Rapson.

Description

Rostrum.—Teeth 6–7/2–3, almost straight, blade uniformly convex, its highest point at 2nd to 3rd teeth; reaching tip of antennular peduncle. Postrostral carina distinctly sulcate, the sulcus slightly less or equal to $\frac{1}{3}$ length carapace. Adrostral carina and sulcus reaching $\frac{2}{5}$ length carapace from posterior edge. Postrostral carina almost reaching posterior border of carapace.

Carapace.—Gastro-orbital carina occupying posterior $\frac{2}{3}$ distance between cervical sulcus and anterior margin carapace. Orbito-antennal sulcus with parallel sides, posteriorly deep; antennal carina $\frac{2}{5}$ length carapace, exceeding orbito-antennal sulcus posteriorly, meeting hepatic sulcus $\frac{1}{3}$ its length from posterior end. Hepatic

carina inclined downwards to horizontal at angle of about 15°, $\frac{1}{5}$ length carapace. Cervical sulcus upcurved, shallow, $\frac{1}{4}$ length carapace.

Antennules.—Upper flagellum longer than lower, and 0·55 length peduncle in ♂, 0·7 in ♀. Prosartema reaching about $\frac{1}{4}$ 2nd segment of antennular peduncle; stylocerite attaining $\frac{1}{2}$ 1st segment.

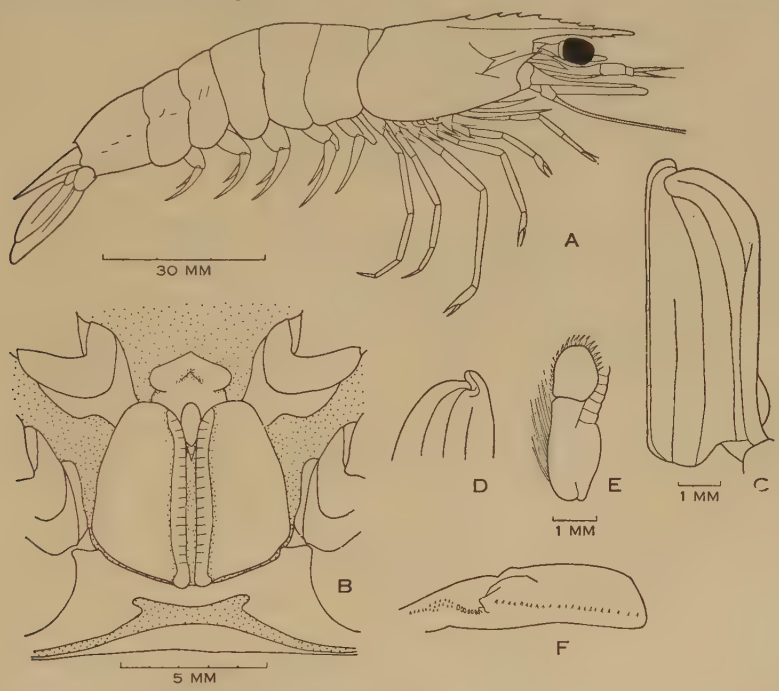

Fig. 6.—*Penaeus semisulcatus* de Haan. *A*, 137 mm ♂; *B*, thelycum 190 mm ♀; *C*, inner aspect of left half of petasma, 137 mm ♂; *D*, outer lateral distal portion of petasma (same scale); *E*, appendix masculina; *F*, cardiac plate and zygocardiac ossicle.

Thoracic appendages.—Dactyl 3rd maxilliped ♂ $\frac{2}{3}$ length propodus which bears an apical tuft of setae as long as dactyl. Third maxilliped reaching as far as or slightly exceeding tip of 1st segment of antennular peduncle; 1st pereiopod exceeding carpocerite by $\frac{1}{2}$ to entire dactyl; 2nd reaching or exceeding tip of 1st, 3rd exceeding 3rd segment of antennular peduncle; 4th exceeding carpocerite by $\frac{1}{2}$ to entire dactyl; 5th very slightly exceeding 4th. Exopods on all pereiopods; an ischial spine, smaller than basial, on 1st.

Abdomen.—Dorsally carinated from anterior 4th somite. Fourth and 5th somites each with 2, 6th with 3 lateral cicatrices. Telson unarmed.

Gastric mill (Fig. 6*F*).—Cardiac plate with 18–23 spinules. Zygocardiac ossicle with principal tubercle + 8–9 smaller tubercles of uniform size, and a long row of irregular spinous tubercles; prepyloric with 9–10 lateral teeth.

Petasma (Fig. 6*C*, *D*).—Median projections flattened dorsoventrally, slightly overhanging lateral lobes; latter with minute apical spines; minutely tuberculate internally and externally but without distinct rows or areas of spines.

Appendix masculina (Fig. 6*E*).—Length distal piece $1\frac{1}{4}$ width, $\frac{1}{2}$ length basal piece.

Thelycum (Fig. 6*B*).—Anterior plate obtusely angled apically, with deep V-shaped excavation; a posterior tongue inserted between flaps of seminal receptacle for $\frac{1}{3}$ their length. Width of anterior plate $\frac{1}{3}$ seminal receptacle at its widest point. Seminal receptacle as wide as long, flaps strongly reflected with transverse striae on everted lips and almost angular at their lateral extremities.

Colour in life.—Dark green with indistinct darker crossbands on the abdomen; antennal scales, eyestalks, pleopods, and uropods dull red, the latter with a brownish fringe; pereiopods with yellow and reddish bands, antennae banded (Racek 1955).

Distribution

Ranging from south-eastern Queensland through Indonesia and Philippine Is. to Japan; and from Singapore through Indus Delta, Madras, and Red Sea to Suez (various authors). This species seems at present to be uncommon in Australian waters, though common in Japanese and Indian markets, sometimes commercially important.

Discussion

P. semisulcatus resembles *P. esculentus* in general facies, but is readily distinguished by the following features:

Feature	*P. semisulcatus*	*P. esculentus*
Postrostral carina	Sulcate	Non-sulcate
Adrostral carina	Extending well beyond epigastric tooth	Reaching epigastric tooth
Hepatic carina	Extending posteriorly for $\frac{1}{3}$ its length beyond junction with antennal carina	Ending at the junction with antennal carina
Fourth and 5th abdominal somites	Each somite with 2 pairs of lateral cicatrices	4th with none, 5th with 1 pair of lateral cicatrices
Petasma	No external spinules on the lateral lobe	An external row of about 20 prominent spinules on lateral lobe

P. semisulcatus has been confused with *P. monodon* (see discussion under this species), but may be separated from it by the following features:

Feature	*P. semisulcatus*	*P. monodon*
Postrostral carina	Fully sulcate	Feebly, or partially sulcate
Rostrum	More or less straight with convex blade	Strongly sigmoidal

Feature	*P. semisulcatus*	*P. monodon*
Adrostral carina	Reaching well beyond epigastric tooth	Reaching to epigastric tooth
Hepatic carina	Distinct, but not strongly elevated, inclined at an angle of 15° to horizontal	Strongly elevated, horizontal
Exopod of 5th pereiopod	Present	Absent

The foregoing description differs from that of Kubo (1949) (for "*P. monodon*") in that the 3rd pereiopod is slightly longer and prepyloric ossicle has 9–10 teeth on each side, the latter being described by Kubo as having but 3 pairs of teeth. It is probable that Kubo has erred in describing the ischial spine as being "on the second limb only", as this does not seem to be a feature characteristic of any *Penaeus* spp. Apart from these features, agreement with Kubo's description is good. Further, this description is not applicable to *P. monodon*, and it seems likely that the 2 species have been confused.

Penaeus esculentus Haswell

Tiger Prawn

Fig. 7*A–E*

Penaeus esculentus Haswell, 1879, p. 38; 1882, p. 200. Kubo, 1949, pp. 315–17. Racek, 1955, pp. 219–20.
Peneus esculentus Schmitt, 1926, pp. 362–5.
Penaeus monodon Whitelegge, 1900, p. 224.

Material.—Wallis Lake, N.S.W., to Townsville, Qld., 14 specimens 60–237 mm; Noosa River, Qld., juveniles 20–60 mm. Material from Exmouth Gulf, Hampton Harbour, and Shark Bay, W.A., and the Australian Museum collection has also been examined.

Description

Rostrum.—5–7/3–4 teeth, usually 6/3; exceeding tip of antennular peduncle in specimens below 5 cm, becoming shorter with age, reaching middle of 2nd segment of antennular peduncle in 23 cm ♀♀; sigmoidal with low blade in juveniles, becoming almost straight with high blade in large specimens. Adrostral carina reaching epigastric tooth, postrostral carina non-sulcate ending $\frac{1}{9}$ length carapace from posterior edge.

Carapace.—Length 1·5 times depth; gastro-orbital carina occupying posterior $\frac{2}{3}$ distance between postorbital margin of carapace and hepatic spine. Hepatic carina distinct but not prominent, very slightly inclined downwards from horizontal axis, barely reaching posterior end of antennal carina. Hepatic and cervical sulci shallow, latter curving upwards posteriorly, ending below epigastric spine and ranging from $\frac{1}{6}$ (Wallis Lake prawns) to $\frac{1}{4}$ length carapace. Cervical carina well defined and extending almost as far as sulcus.

Antennules.—Flagella subequal, $\frac{2}{3}$ length peduncle. Prosartema reaching basal $\frac{1}{3}$ to $\frac{1}{2}$ 2nd segment; stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Third maxilliped exceeding basal segment of antennular peduncle by dactyl, ♂ with apical tuft of setae on propodus, extending as far as slightly hollowed dactyl which is inserted subapically, with a large subapical tuft of setae on carpus. Dactyl $\frac{2}{3}$ length propodus in ♂ and ♀. First pereiopod exceeding carpocerite by dactyl, 2nd reaching end of basal segment of antennular peduncle, 3rd reaching tip of peduncle, 4th and 5th exceeding carpocerite by $\frac{1}{2}$ dactyl. An ischial spine on 1st pereiopod; 5th with a small exopod.

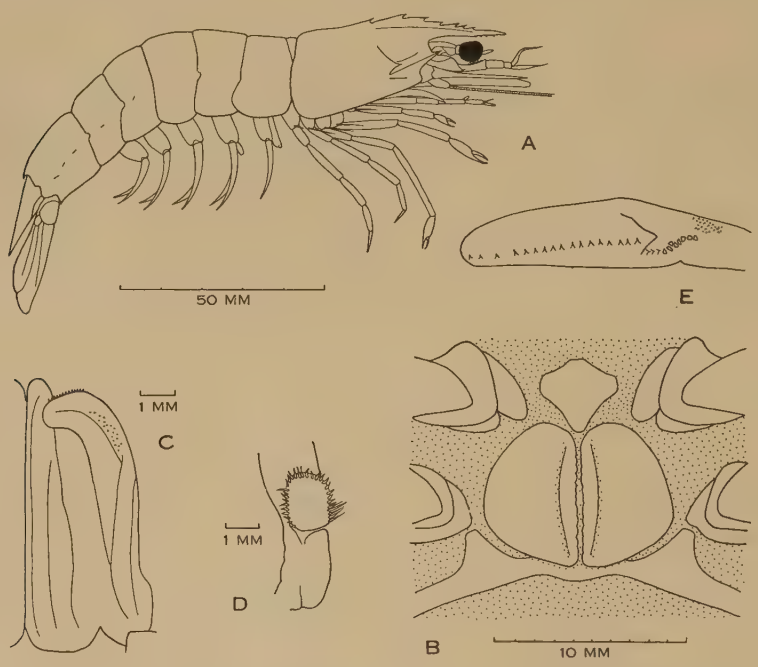

Fig. 7.—*Penaeus esculentus* Haswell. *A*, 141 mm ♂; *B*, thelycum of 230 mm ♀; *C*, inner aspect of left half of petasma, 141 mm ♂; *D*, appendix masculina of same; *E*, cardiac plate and zygocardiac ossicle.

Abdomen.—Dorsally carinated from $\frac{1}{2}$ 4th somite, carina curving downwards strongly towards end of 6th somite; 5th with a small, barely perceptible cicatrice, 6th with 3 ill-defined cicatrices. Telson unarmed.

Gastric mill (Fig. 7*E*).—Cardiac plate with 16–18 spinules; zygocardiac ossicle with principal + 9–12 conical teeth and a cluster of minute teeth; prepyloric with 8–9 lateral teeth.

Petasma (Fig. 7*C*).—Lateral lobes with a number of minute distal setae and an irregular lateral external row of about 20 spinules.

Thelycum (Fig. 7*B*).—Length of anterior plate $1\frac{1}{2}$ width, concave and pear-shaped, apex barely inserted between flaps of seminal receptacle. Seminal

receptacle more or less circular, flaps forming tumid lips on mid line, inner edges tending to be serrated in large impregnated females.

Appendix masculina (Fig. 7*D*).—Length distal piece $1\frac{1}{5}$ width.

Colour in life (*mature prawns living in open waters*).—Carapace and abdomen transversely banded, those of abdomen mid brown, 2 to each somite, the anterior much lighter; spaces between bands buff to yellow. Rostrum with red and brown alternating bands. Antennae with alternating mid-brown and white bands. Bases of pleopods yellow with tinge of blue. Uropods brown changing distally to yellow. Fringing setae of uropods and tips of other appendages dark red. *Juvenile prawns in estuaries* (usually in *Zostera* beds) tend to be irregularly mottled with dark and light brown with intervening light-coloured patches.

Distribution

Wallis Lake, N.S.W., to Shark Bay, W.A.; Borneo (Kubo 1949). Trawled commercially in Queensland, and appearing sporadically in commercial quantities off Evans Head, N.S.W. Average size at sexual maturity in tropical waters (Exmouth Gulf), ♂ 145 mm, ♀ 155 mm.

Discussion

The above description differs from that of Haswell regarding length of the antennular flagella. Schmitt (1926), who examined a cotype, stated that the filamentous portions of all 4 flagella were missing and that the basal portion equalled the last 2 segments of the peduncle in length. In Schmitt's figure length of the flagella corresponds with that in Moreton Bay and Townsville specimens. Only among the larger of these prawns do rostra correspond with Schmitt's description. In immature prawns as noted, the general shape resembles that of *P. monodon*. The following features are useful for distinguishing *P. esculentus* and *P. monodon*:

Feature	*P. esculentus*	*P. monodon*
Postrostral carina	Non-sulcate	Usually sulcate or indications thereof
Gastro-orbital carina	Occupying the posterior $\frac{2}{3}$ distance between postorbital margin of carapace and hepatic spine	Occupying posterior $\frac{1}{3}$ distance between post-orbital margin carapace and hepatic spine
Hepatic carina	Barely reaching posterior end of antennal carina	Extending posteriorly past end antennal carina by $\frac{1}{3}$ its length
Fifth pereiopod	Exopod present	Exopod absent
Colour	Without any trace of blue	Blue coloration usually present

Penaeus merguiensis de Man

White or Banana Prawn

Fig. 8*A–I*

Penaeus merguiensis de Man, 1888, pp. 287–90; 1911, pp. 104–5. Kubo, 1949, pp. 308–11. Racek, 1955, pp. 221–2.

Peneus merguiensis Schmitt, 1926, pp. 360–1. Boone, 1935, pp. 96–101.

Penaeus indicus var. *merguiensis* Alcock, 1905, p. 515; 1906, p. 13.

Penaeus indicus Bate, 1888, p. 248. De Man, 1892, p. 511; 1898, p. 680.

Material.—QUEENSLAND: Brisbane River to Norman River, Gulf of Carpentaria, 38 specimens, 10–223 mm. WESTERN AUSTRALIA: Exmouth Gulf, 6 specimens, 152–166 mm. Australian Museum collection.

Description

Rostrum (Fig. 8*A–D*).—Teeth, 5–8/2–5, usually 6–7/4–5. Long, slender, upcurving, $1\frac{1}{2}$ to twice length carapace in postlarvae; 1st 5 dorsal teeth close together, penultimate and distal tooth widely separated; position of latter variable, at $\frac{1}{2}$ length of rostrum when there are 6, and $\frac{1}{3}$ from tip when there are 7, but sometimes varying regardless of number of teeth. Becoming shorter with increasing size, equalling length carapace in prawns of 80 mm, almost straight and with higher blade. Rostrum not exceeding 2nd segment of antennular peduncle in large prawns, blade high of broad triangular form. Adrostral carina usually ending between 1st and 2nd teeth, sometimes reaching 1st. Postrostral carina ending at posterior $\frac{1}{5}$ carapace.

Carapace.—Glabrous, thin, sulci and carinae feebly defined. Gastro-orbital carina absent or feeble, occupying middle $\frac{1}{3}$ distance between hepatic spine and postorbital margin; orbito-antennal sulcus wide and ill defined; antennal carina ending in front of hepatic spine, hepatic carina absent. Cervical sulcus $\frac{1}{6}$–$\frac{1}{7}$ length carapace.

Antennules.—Outer flagellum $1\frac{1}{2}$ to twice length inner, longer than peduncle. Prosartema exceeding tip, stylocerite barely reaching $\frac{1}{2}$ basal segment.

Thoracic appendages.—Endopod 3rd maxilliped reaching tip of antennular peduncle in adult ♂, usually not exceeding basal segment in ♀; dactyl $\frac{1}{2}$ propodus, inserted subapically in ♂ with apical tuft of setae reaching $\frac{1}{2}$ dactyl. First pereiopod exceeding carpocerite by dactyl, 2nd reaching tip of 2nd segment antennular peduncle, 3rd exceeding 3rd antennular segment by at least dactyl, 4th and 5th exceeding carpocerite by dactyl. Ischial spine on 1st pereiopod.

Abdomen.—Dorsally carinated from middle of 4th somite in larger prawns, on 5th and 6th only in specimens below 80 mm. Fifth somite with 1, 6th with 3 small lateral cicatrices. Telson unarmed.

Gastric mill (Fig. 8*I*).—Cardiac plate with 22–28, usually 24 spinules. Zygocardiac ossicle with principal + 7–10 smaller teeth and longitudinal row of very small teeth. Prepyloric acute with 7–9 separated lateral teeth.

Petasma (Fig. 8*F*, *G*).—Median distal projections not overhanging lateral lobes when seen from side. Distal tip of lateral lobe minutely serrate, outer surface of lobe with large number of minute conical teeth.

Appendix masculina (Fig. 8*H*).—Length distal piece 1–1$\frac{1}{4}$ times width, $\frac{3}{4}$ length basal piece.

Thelycum (Fig. 8*E*).—Anterior plate slightly concave, $\frac{1}{4}$ length seminal receptacle, with posterior convex projection, inserted between flaps of seminal receptacle for $\frac{1}{3}$ length. Seminal receptacle round with two flaps forming tumid lips on mid line.

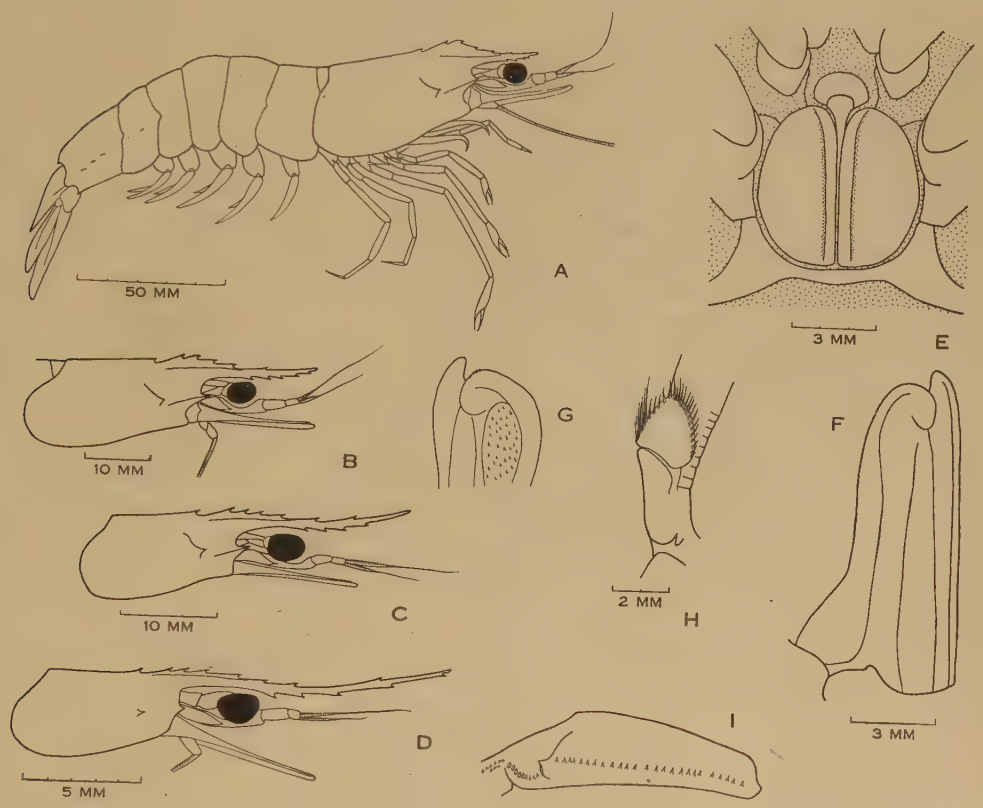

Fig. 8.—*Penaeus merguinensis* de Man. *A*, 156 mm ♀; *B*, cephalothorax, 118 mm ♂; *C*, cephalothorax, 74 mm ♂; *D*, cephalothorax, 35 mm ♀; *E*, thelycum, 180 mm ♀; *F*, inner aspect of right half of petasma, 179 mm ♂; *G*, outer lateral distal half of petasma, 179 mm ♂ (same scale); *H*, appendix masculina; *I*, cardiac plate and zygocardiac ossicle.

Colour in life (*mature prawns living in open waters*).—Body cream to yellow, sometimes minutely speckled with blue; rostral blade often blue; antennules banded with brown; antennae red; legs and pleopods yellowish, sometimes with brown or pink tinge; abdominal carina brownish red, sometimes blue; uropods brown tipped with yellow, sometimes with blue. Body sometimes pink to red, especially when coming from deeper waters. *Juveniles in muddy estuaries*.—Body cream, speckled with blue, rostral tip dark brown, outer edges of antennal scales, abdominal carina, telson, and uropods often more or less brown. *Postlarvae*.—Body white to cream, tip of rostrum dark brown.

Distribution

Australia, Ballina, N.S.W., to Exmouth Gulf, W.A., Philippine Is., Makassar, Java Sea, Mergui Archipelago, Karachi, Bombay, Palk Strait, Orissa and Ganjam, Hooghly Delta (de Man 1911); Batavia, Singapore (Kubo 1949). Trawled commercially, Queensland and Western Australia. Juveniles found up to 24 miles from mouth of Brisbane River, with juveniles of *Metapenaeus mastersii*. Average size at sexual maturity in tropical waters (Exmouth Gulf) ♂ 150 mm, ♀ 160 mm.

Discussion

This species is similar to *Penaeus indicus* Milne Edwards, but though adults have distinctive rostra, the progressive relative shortening of the rostrum during development makes immature specimens of these 2 species difficult to distinguish. De Man (1911) uses the position of the last rostral tooth to separate the juveniles, but de Man's 2 criteria are included in the range found within *P. merguiensis*. *P. indicus* var. *longirostris* de Man (1892, 1911) is likely to be juvenile *P. indicus*, possibly with a longer rostrum than is usual for specimens of this size (125–165 mm). In some juvenile *P. indicus* from Ceylon, about 100 mm long, the rostrum is longer than the carapace, with distinct sigmoidal curve and low upper blade. *P. merguiensis* of comparable size has a relatively straight rostrum with a higher upper blade. In some specimens in the Australian Museum, labelled "Dr. Day collection Karachi", the adrostral carina reaches 1st rostral tooth, and there is a distinct though feeble gastro-orbital carina, occupying middle $\frac{1}{3}$ between rim of the carapace and hepatic spine. The latter feature was not present in any Australian material examined.

The following features seem the most reliable for separating the 2 species:

Feature	*P. merguiensis*	*P. indicus*
Adrostral carina	Not reaching 1st rostral tooth in Australian specimens	Reaches 1st rostral tooth
Gastro-orbital carina	Absent in Australian specimens (see discussion above for exception)	Well defined, occupying posterior $\frac{2}{3}$ distance between hepatic spine and margin of carapace
Outer antennular flagellum	Shorter than carapace	Longer than carapace
Dactyl of 3rd maxilliped in adult ♂	Half length of propodus	As long as propodus

Racek (1955) records *P. indicus* on the east coast of Australia. The writer has not yet examined any of this species collected from Australian waters. It is probably not common, though its presence is to be expected, especially on the north coast of Australia.

Genus FUNCHALIA Johnson

Funchalia Johnson, 1867, p. 895. Bouvier, 1908, p. 91. Lenz and Strunck, 1914. Calman, 1925, pp. 10–11. Burkenroad, 1934*b*, pp. 76–7; 1936, pp. 126–9; 1940, p. 36. Barnard, 1950, pp. 608–9.
Aristeus Bate, 1888 (part), p. 309.
Penaeus Faxon, 1895 (part). Lenz and Strunck, 1914 (part).
Hemipenaeopsis Bouvier, 1905, p. 981.
Grimaldiella Bouvier, 1905, p. 982.

Rostrum with or without ventral rostral teeth; no orbital angle; antennal spine present or absent; branchiostegal spine present; hepatic spine sometimes absent; branchiocardiac and inferior carinae prominent; cervical and orbito-antennal sulci feeble or absent. Fifth and 6th abdominal somites with prominent lateral carinae; terga of 1st to 4th often with carinae; telson with 3 pairs of fixed subapical spines. Upper antennular flagellum longer than the carapace; no spine on ventral disto-median edge of 1st segment. Incisor process of mandible elongate, scimitar-like, and lying transversely behind labrum. Second maxilla with 3 endites; spines on basis and ischium of 1st and 2nd legs; small exopods on all pereiopods. Exopod of uropod with large external spine. Petasma simple, open, often asymmetrical. Thelycum simple, with deep seminal receptacle, open or closed by paired flaps.

Key to the Species of Funchalia

1. Rostrum with ventral teeth, antennal spine absent ..... *F. balboae* (Faxon)
   Rostrum without ventral teeth; antennal spine present 2
2(1). Hepatic spine present in adults; with more than 10 rostral teeth 3
   Hepatic spine absent in adults; with fewer than 10 rostral teeth 4
3(2). Sixth abdominal somite with a short carina below and parallel to the long mid-lateral carina; seminal receptacle open ..... *F. woodwardi* Johnson
   Sixth abdominal somite with a long mid-lateral carina only; seminal receptacle closed by a pair of flaps ..... *F. danae* Burkenroad
4(2). Petasma with small triangular projection on ventral surface of free distal part of larger endopod; thelycum with small median ridge behind seminal receptacle ..... *F. villosa* (Bouvier)
   Petasma without projection on ventral surface of free distal part of larger endopod; thelycum with large median tooth-like tubercle behind seminal receptacle ..... *F. taaningi* Burkenroad

Funchalia villosa (Bouvier)

Fig. 9*A–E*

Hemipenaeopsis villosus Bouvier, 1905 (part).
Grimaldiella richardi Bouvier, 1905 (part).
Funchalia woodwardi Bouvier, 1908 (part), p. 93. Lenz and Strunck, 1914.
Funchalia vanhöffeni Lenz and Strunck, 1914.
? *Funchalia* Gurney, 1924.

Material.—Lord Howe I.: Aust. Mus. regd. No. P6762, 7 ♂, 59–74 mm (carapaces 12·5–15·5 mm), 8 ♀, 58–86 mm (carapaces 12·5–19 mm).

Description

Rostrum.—Teeth 4–5 + epigastric; not reaching as far as or slightly exceeding cornea, free part slightly depressed; adrostral carina feeble, ending below 1st tooth,

the shallow sulcus ending just behind epigastric; postrostral carina ending at $\frac{1}{9}$ carapace; 2nd tooth above postorbital rim of carapace.

Carapace.—Gastrofrontal sulcus feeble, indistinct anteriorly, reaching $\frac{1}{2}$ carapace; antennal spine small, carina and orbito-antennal sulcus reaching $\frac{1}{4}$ carapace; branchiostegal spine slightly above the barely acute pterygostomial angle; carina behind branchiostegal reaching $\frac{1}{3}$ distance between spine and inferior carina. Hepatic spine absent, sulcus running from margin of carapace becoming confluent with inferior sulcus, latter reaching branchiostegal margin. A feeble carina and sulcus arising vertically from branchiocardiac carina just behind $\frac{1}{2}$ carapace, curving forward, sulcus becoming confluent with feeble cervical sulcus; a short feeble sulcus parallel and anterodorsal to latter. A short oblique carina and sulcus on postero-dorsal surface carapace.

Antennules.—Upper flagellum as long as carapace + rostrum, lower $\frac{3}{5}$ upper. Prosartema reaching 0·7 basal segment; stylocerite a triangular flat plate reaching $\frac{1}{2}$ cornea.

Mandible.—Incisor process reaching the opposite branchiostegite, almost as long as palp.

Thoracic appendages.—Third maxilliped reaching as far as carpocerite; 1st pereiopod exceeding pterygostomial angle by dactyl; 2nd reaching $\frac{1}{2}$ carpocerite; 3rd exceeding it by dactyl; 4th reaching base, 5th reaching $\frac{3}{4}$ carpocerite, dactyls of both curved and slender.

Abdomen.—First somite with downcurving continuation of branchiocardiac carina; pleura of 1st to 4th somites with vertical carinae; lateral carina of 5th and 6th continuing on 4th, sloping obliquely towards dorsum; carina and sulcus on ventral margin of 6th pronounced. A small elongate tubercle on dorsum of 2nd and 3rd somites, 4th to 6th with a carina ending in a small tooth. Telson with 2 lobes on either side of base, the more proximal partly cleft. Inner uropod exceeding telson, which reaches $\frac{2}{3}$ outer. Prominent sternal keels between 1st and 2nd pleopods.

Gastric mill (Fig. 9*E*).—Cardiac plate long, narrow, with dense ventral fringing setae, without row of median teeth; zygocardiac ossicle a flattened tooth with minute lateral spinules; immediately behind zygocardiac, a rounded process densely covered with spinules; prepyloric ossicle with slightly concave edge bearing a double row of spinules; urocardiac suboval, deeply concave; cardiac and pterocardiac ossicles absent.

Petasma (Fig. 9*B*).—Asymmetrical, reaching bases of 4th pereiopods; either right or left endopod larger than other; the smaller with simple grooved spatulate apex; apex of the larger deeply grooved, curving dorsally, with paired blunt lateral lobes, with proximal triangular projection on outer edge. A pair of hoof-like projections on pleopods proximal to articulation with petasma.

Appendix masculina (Fig. 9*C*).—Distal segment with oval, flattened, expanded apex, slightly excavate with small anterior tubercle and with marginal row of short setae.

Thelycum (Fig. 9*D*).—Anterior plate between and above coxae of 4th pereiopods, cordiform with sharp apex and medially grooved, the lateral edges curving ventrally.

Sternal plate of 5th pereiopods large, flat, quadrangular with 2 anterior extensions fusing with anterior plate to form the deep seminal receptacle; extensions continuing backwards as carinae curving laterally behind 5th coxae along edges of sternite. A small elongate median tubercle between 5th coxae.

Distribution

Tropical Atlantic (Burkenroad 1936). The larva from New Zealand described by Gurney (1924) may be *F. villosa*, but excepting this, the Lord Howe I. specimens are the first Indo-Pacific record of this species.

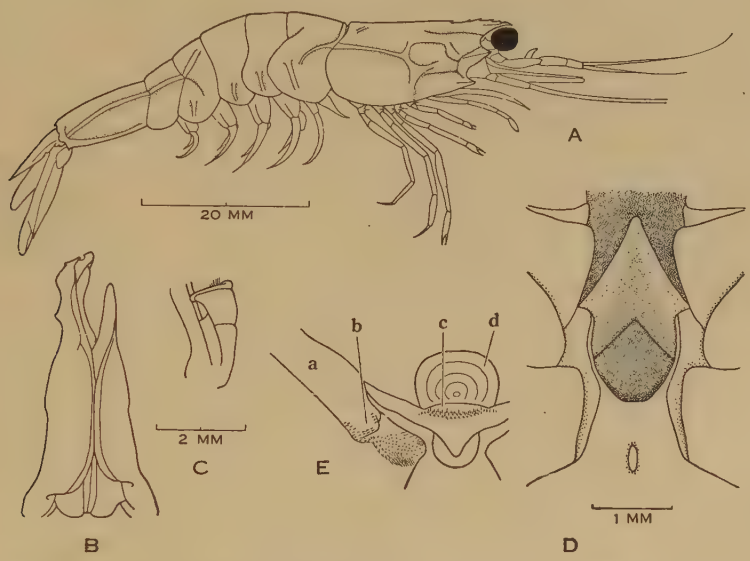

Fig. 9.—*Funchalia villosa* (Bouvier). *A*, 74 mm ♂; *B*, petasma, 74 mm ♂; *C*, appendix masculina, 74 mm ♂; *D*, thelycum, 76 mm ♀; *E*, ossicles of gastric mill (*a*, cardiac plate; *b*, zygocardiac ossicle; *c*, prepyloric ossicle; *d*, urocardiac ossicle).

Discussion

The present specimens agree with Burkenroad's (1936) description, except that some have only 4 rostral teeth, and all have the dorsal abdominal carina ending in a small tooth, whereas Burkenroad's specimens had a "long tooth." *F. taaningi* Burkenroad (1940) differs in only minor features of petasma, thelycum, and in position of branchiostegal spine from *F. villosa*.

All *Funchalia* spp. have so far been collected in the open ocean, often from considerable depths. The greatly elongate incisor processes of the mandibles and sculpturing of the integument set *Funchalia* spp. apart from other Penaeinae. In *F. villosa* these incisor processes, together with the talon-like dactyls of 4th and 5th pereiopods, and absence of teeth in the gastric mill, suggest that the species may feed by piercing and sucking the body fluids of some pelagic animal. Whether *F. villosa* is predatory, as the large hemispherical corneas seem to indicate, or merely attaches to some relatively passive organism has yet to be discovered.

Genus METAPENAEOPSIS Bouvier

Metapenaeopsis Bouvier, 1905. Kubo, 1949, pp. 408–11.
Penaeopsis de Man, 1911 (part), pp. 53–5, 61. Balss, 1914 (part), pp. 6–7. Kemp, 1915 (part), p. 321. Schmitt, 1926 (part), pp. 319–23. Burkenroad, 1934*a* (part), pp. 4–12. Barnard, 1950, p. 592.
Leptopenaeus Kishinouye, 1929, p. 282.
Ceratopenaeus Kishinouye, 1929, p. 282.
Erthyropenaeus Kishinouye, 1929, p. 283.
Metapeneus Alcock, 1906 (part), p. 16.

Rostrum dorsally toothed only. Carapace without longitudinal or transverse sutures. Cervical, hepatic, and orbito-antennal sulci usually ill defined. Orbital, antennal, hepatic, and pterygostomial spines well developed. Telson with a pair of fixed subapical spines followed by several pairs of large movable spines. Cornea often large. First antennular segment with a spine, which may be vestigial, on ventral distomedian border. Antennular flagella variable in length, sometimes longer than carapace. Maxillulary palp unsegmented. Basial spines on 3rd maxilliped and 1st and 2nd pereiopods. Exopods on all pereiopods. Petasma asymmetrical, divided transversely at about $\frac{1}{2}$ its length into proximal and distal portions, the latter complex and further divided into lobules and projections (Fig. 11*B*, *C*). Appendix masculina usually consisting of basal piece only, distal piece if present small. Thelycum consisting of a transverse plate between coxae of 4th pereiopods, and variable structures between this plate and posterior transverse elevation of last thoracic sternite. Zygocardiac ossicle consisting of 2 large teeth, sometimes with smaller teeth and a patch of minute teeth. Pleurobranchiae on 3rd to 7th thoracic somites; a rudimentary arthrobranch on 1st, anterior and posterior arthrobranchiae on 2nd to 6th, and a rudimentary anterior and a posterior arthrobranch on 7th thoracic somites; mastigobranchiae on 1st, 2nd, and 4th to 6th thoracic somites; carapace usually pubescent.

Kubo (1949) elevates subgenus *Metapenaeopsis* as defined by Burkenroad (1934*a*) to generic rank, to separate species with an asymmetrical petasma from those included in *Penaeopsis* Bate (restricted).

Metapenaeopsis is a large genus, and contains a number of obscure and doubtful species. Many are small and uncommon and this possibly accounts for the fact that many species are little known. The type species, *M. pubescens* Bouvier, is from the tropical Atlantic, and 4 additional species, 2 from America, are described from the Atlantic. (For key to Atlantic and Pacific American spp. see Anderson and Lindner (1945).) The majority (19) of Indo–West Pacific *Metapenaeopsis* spp. are keyed below. The following little-known or doubtful species have not been included: *M. assimilis* (de Man), 1920; *M. batei* (Miers), 1884; *M. commensalis* (Borradaile), 1898 (de Man (1911) states that the single type of this species, of which only ♂ is known, has been lost); *M. gallensis* (Pearson), 1905. *M. longipes* (Paulson), 1875, *M. consobrinus* (Nobili), 1904, *M. perlarum* (Nobili), and *M. vaillanti* (Nobili) are from the Red Sea, the last 3 very possibly being *Metapenaeus* spp. and synonymous with well-known species.

According to the rules of grammar, *Metapenaeopsis* should be of feminine gender. Most authors have treated it as of masculine gender, and as there is a possibility

of the gender being decided by the International Commission of Zoological Nomenclature (Dr. L. B. Holthuis, personal communication), *Metapenaeopsis* has been treated as of masculine gender in the present paper.

Key to the Indo-West Pacific Species of Metapenaeopsis

1. Length 6th pleonic somite less than twice depth near posterior end; spine on distoventral border of basal segment of antennular peduncle vestigial 2
   Length 6th pleonic somite more than twice depth near posterior end; spine on the distoventral border of basal segment of antennular peduncle usually well developed 14

2(1). Stridulating organ present on posterior branchiostegite 3
   Stridulating organ absent from posterior branchiostegite 6

3(2). Dorsal carina of 3rd abdominal somite with well-defined sulcus ..... *M. durus* Kubo
   Dorsal carina of 3rd abdominal somite flat or feebly sulcate at posterior end only 4

4(3). Rostrum reaching to or almost to tip of antennular peduncle; plate of thelycum between 4th pereiopods wider than long, and much larger than coxal projections 5
   Rostrum reaching to distal end of 1st segment of antennular peduncle; plate of thelycum between 4th pereiopods as long as wide and about as large as coxal projections .... *M. acclivis* (Rathbun)

5(4). Stridulating organ with 13–25 (usually 18–22) ridges; inner intermediate strip of petasma exceeding outer; rim of posterior transverse sternal ridge thelycum with median protuberance ..... *M. barbatus* (de Haan) (=*P. akayebi* Rathbun)
   Stridulating ridge with 7–12 ridges; inner intermediate strip of petasma as long as or shorter than the outer; rim of posterior transverse sternal ridge thelycum without median protuberance ..... *M. novae-guineae* (Haswell)

6(2). Epigastric tooth at ¼ carapace; antennal scale more than twice as long as broad 7
   Epigastric tooth a little posterior to middle of carapace; antennal scale twice as long as wide ..... *M. lamellatus* (de Haan)

7(6). With transverse plates only between coxae of ♀ 4th and 5th legs 8
   With 2 median spines situated one behind the other between coxae of ♀ 4th and 5th legs ..... *M. evermanni* (Rathbun)

8(7). A pair of long spinous processes on sternum between coxae of ♀ 2nd pereiopods 9
   No spinous processes on sternum between coxae of ♀ 2nd pereiopods .. *M. velutinus* (Dana)

9(8). Hepatic sulcus descending almost vertically to ventral edge of branchiostegite .... *M. borradailei* (de Man)
   Hepatic sulcus absent or not reaching to ventral edge of branchiostegite 10

10(9). Anterior transverse plate between ♀ 4th legs with 1 or more pairs of median prominent teeth-like processes immediately posterior to it 13
   Anterior transverse plate between ♀ 4th legs without 1 or more pairs of median teeth-like processes immediately posterior to it 11

11(10). Anterior transverse sternal ridge between ♀ 5th pereiopods with pair of spinous anterolateral processes; process between 3rd legs either double or absent 12
   Anterior transverse sternal ridge between ♀ 5th pereiopods without pair of spinous anterolateral processes; a single spinous process between 3rd legs .... *M. quinquidentatus* (de Man)

12(11). Posterior transverse sternal ridge between ♀ 5th pereiopods with large median triangular process; no processes between 3rd legs ..... *M. dalei* (Rathbun)
   Posterior transverse sternal ridge between ♀ 5th pereiopods with small median tubercle; a pair of bluntly pointed processes between 3rd legs ..... *M. incomptus* Kubo

13(10). Thelycum with a pair of small pointed processes immediately behind plate between 4th pereiopods, and arising from posterior base of these processes, a pair of acute dentiform tubercles ..... *M. distinctus* (de Man)
   Thelycum with a pair of more or less diverging processes immediately behind plate between 4th pereiopods, and with no acute tubercles at posterior base .... *M. mogiensis* (Rathbun) (=*Penaeopsis hilarulus* de Man)

14(1). Anterior plate of thelycum with posterior extension 15
Anterior plate of thelycum without posterior extension .....*M. sinuosus*, sp. nov.
15(14). Posterior extension of anterior plate of thelycum bilobed 16
Posterior extension of anterior plate of thelycum single and pointed 18
16(15). Rostrum as long as or longer than antennular peduncle 17
Rostrum not reaching tip of antennular peduncle .....*M. coniger* (Wood-Mason)
17(16). Right apex of petasma slightly exceeding the left .....*M. sibogae* (de Man)
Left apex of petasma slightly exceeding the right .....
M. phillippii (Bate) (=*Penaeus phillipinensis* (Bate 1888) (=*Penaeopsis coniger andamanesis* (Wood-Mason & Alcock))
18(15). Abdomen dorsally carinated posterior to 1st somite .....*M. latus* Kubo
Abdomen dorsally carinated posterior to 2nd somite .....*M. kyushuensis* (Yokoya)

Metapenaeopsis durus Kubo

Fig. 10*A*, *B*

Metapenaeopsis durus Kubo, 1949, pp. 421–4, figs. 8A, 18G-L, 22O, 46D, 64C, 76E, J, 80L, 148C, 149.

Material.—WESTERN AUSTRALIA: Near entrance Roebuck Bay, Broome, ♀ 59 mm; between C. Bossuet and Broome, ♀ 61 mm.

Description

Rostrum.—Teeth 8–9 + epigastric; almost reaching tip of antennular peduncle, slightly upcurved. Adrostral carina reaching postorbital rim of carapace and following it for a short distance. Epigastric tooth at $\frac{1}{3}$ carapace; postrostral carina absent.

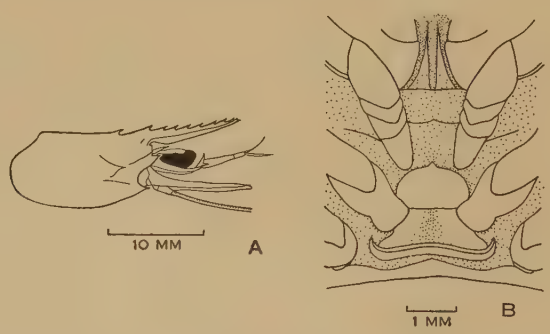

Fig. 10.—*Metapenaeopsis durus* Kubo. *A*, cephalothorax, 59 mm ♀; *B*, thelycum, 59 mm ♀.

Carapace.—Orbital spine small; orbito-antennal sulcus shallow. A postocular depression present. Antennal spine large, reaching cornea; carina short, reaching barely $\frac{1}{3}$ distance between tip of spine and hepatic spine. Cervical and hepatic sulci indistinct owing to presence of dense pubescence; when this is removed sulci are distinct and deep. Cervical sulcus straight, reaching $\frac{1}{2}$ carapace; hepatic sulcus horizontal below spine turning towards pterygostomial spine in front of hepatic, reaching $\frac{2}{3}$ distance between hepatic and pterygostomial spines. Pterygostomial spine reaching almost as far as spine of basicerite. Stridulating ridges on branchiostegite 14–18.

Antennules.—Flagella $\frac{1}{3}$ length peduncle, slightly more than $\frac{1}{4}$ length carapace. Prosartema not reaching as far as eye; stylocerite as long as 1st segment.

Thoracic appendages.—Third maxillipeds reaching from base to $\frac{1}{2}$ 2nd antennular segment. First pereiopod reaching $\frac{1}{2}$ carpocerite, 2nd exceeding it by dactyl; 3rd exceeding 1st antennular segment by dactyl; 4th reaching as far as 1st, 5th exceeding carpocerite by $\frac{1}{2}$ dactyl. Exopod 3rd maxilliped reaching $\frac{2}{3}$ merus; exopods on all pereiopods exceeding ischia. Ischial spine on 1st pereiopod.

Abdomen.—Dorsal carina beginning on posterior $\frac{1}{2}$ 2nd somite, bearing a well-defined sulcus on 3rd somite; carina prominent on 4th to 6th somites; 6th somite 1·7 times as long as deep. Telson as long as inner and outer uropods, with 3 pairs of long lateral spines.

Gastric mill.—Cardiac plate with 32 teeth; zygocardiac ossicle with principal teeth + 3 blunt tubercles. Prepyloric with 7–8 long blunt teeth subequal to median tooth.

Thelycum (Fig. 10*B*).—A pair of long spines between coxae of 2nd pereiopods; no appreciable projections between 3rd. Transverse plate between 4th pereiopods suboval with mucronate anterior edge and as long as broad. Coxal projections of 4th pereiopods rounded, smaller than transverse plate, bounding and slightly overlying a quadrangular plate with broad median depression; posterior sternal plate between 5th pereiopods with a median, broadly triangular, and 2 lateral rounded projections.

Distribution

Tokyo, Miya, Aichi Prefecture (Kubo 1949). Vicinity of Broome, W.A.

Discussion

The present specimens differ from those described by Kubo (1949) in the following features:

Feature	Broome Specimens	Japanese Specimens
Rostrum	Almost reaching tip of antennular peduncle and slightly upturned	Hardly reaching $\frac{1}{2}$ 2nd antennular segment and strongly upturned
Antennular flagella	Barely $\frac{1}{3}$ length carapace	Half length carapace
Number of stridulating ridges	14–18	28–35

The coxal projections of 4th pereiopods are not as large as those figured by Kubo, but this may be due to the smaller size of the Broome specimens (Japanese specimens range from 76·1 to 94·5 mm). Against this the ovaries of the 61 mm female contain formed eggs indicating sexual maturity. Kubo examined only 5 specimens and it is possible that a larger number would show wide variations in rostrum etc. (cf. *M. novae-guineae*). It is possible that the present specimens belong

to a new species, but in the absence of a better series, including males, it is thought advisable, as the majority of features are in close agreement, to include them with *M. durus*.

Metapenaeopsis novae-guineae (Haswell)

Fig. 11*A–F*

Penaeus novae-guineae Haswell, 1879, p. 43; 1882, p. 203.
Penaeus palmensis Haswell, 1879, p. 43; 1882, p. 204.
Penaeus velutinus Bate, 1888, p. 253.
Metapeneus palmensis Alcock, 1906, p. 51.
Metapeneus stridulans Alcock, 1906, p. 27.
Penaeopsis palmensis de Man, 1911, pp. 8, 55, 73.
Penaeopsis stridulans de Man, 1911, p. 65.
Penaeopsis novae-guineae Schmitt, 1926, pp. 338–48. Racek, 1955, pp. 226–7.

Material.—Moreton Bay, Qld., to Exmouth Gulf, W.A., 33 specimens, 38–106 mm. Australian Museum collection.

Description

Rostrum.—Variable, teeth 5–8 + epigastric; usually reaching to, or almost to tip of antennular peduncle, but often much shorter. Postrostral carina often absent, but sometimes a feeble carina reaching $\frac{1}{2}$ carapace. Position of epigastric tooth varying from $\frac{1}{5}$ to $\frac{1}{4}$ carapace, 2nd tooth at frontal margin carapace. Rostral shape variable, ventral margin always upcurved, upper surface sometimes straight and horizontal, sometimes strongly upcurved.

Carapace.—Orbital spine minute; orbito-antennal sulcus sometimes clearly though feebly defined to hepatic spine, but sometimes barely defined at all. Hepatic spine small, with very feeble indication of cervical groove immediately above it. Antennal spine large, without carina. Hepatic sulcus shallow, tomentose, horizontal, slightly below and behind hepatic spine. A stridulating ridge on posterior branchiostegite, with 7–12 ridges varying greatly in size and shape.

Antennules.—Upper flagellum slightly shorter than lower which is $\frac{2}{5}$ peduncle and $\frac{1}{3}$ length carapace in ♂, $\frac{1}{4}$ peduncle and $\frac{1}{5}$ carapace in ♀. Prosartema reaching as far as eye; stylocerite reaching to or almost to tip basal segment.

Thoracic appendages.—Third maxilliped reaching from base to tip of 3rd segment of antennular peduncle; 1st pereiopod reaching almost to, or exceeding, tip of carpocerite; 2nd exceeding it by dactyl to entire propodus; 3rd ranging from base to tip of 2nd segment of antennular peduncle; 4th reaching as far as carpocerite, 5th exceeding it by dactyl to $\frac{1}{2}$ propodus. Ischial spine on 1st pereiopod.

Abdomen.—Second abdominal somite with short feeble dorsal carina, 3rd to 6th with a strong carina, that of 3rd dorsally flat or feebly sulcate posteriorly. Telson with 3 pairs of lateral movable spines, 1st smaller than long 2nd and 3rd and based at $\frac{1}{2}$ telson. Inner uropod as long as telson, slightly exceeded by exopod.

Gastric mill (Fig. 11*F*).—Cardiac teeth 26–32. Zygocardiac ossicle with principal + 2–3 smaller teeth beside upper tooth. Prepyloric with 8–11 long blunt lateral teeth, similar in size to median tooth.

Petasma (Fig. 11*B*, *C*).—Shape of various parts variable and reaching coxae of 4th pereiopods; right distoventral projection (*a*) bearing few small distal processes, left distoventral projection (*e*) with 8–14 larger finger-like processes; both projections much thickened distally. Inner intermediate strip (*g*), usually finger-like and cylindrical, outer intermediate strip (*h*) with numerous minute distal setae, as long as the inner strip in Moreton Bay ♂♂, much longer in Townsville and Western Australian specimens.

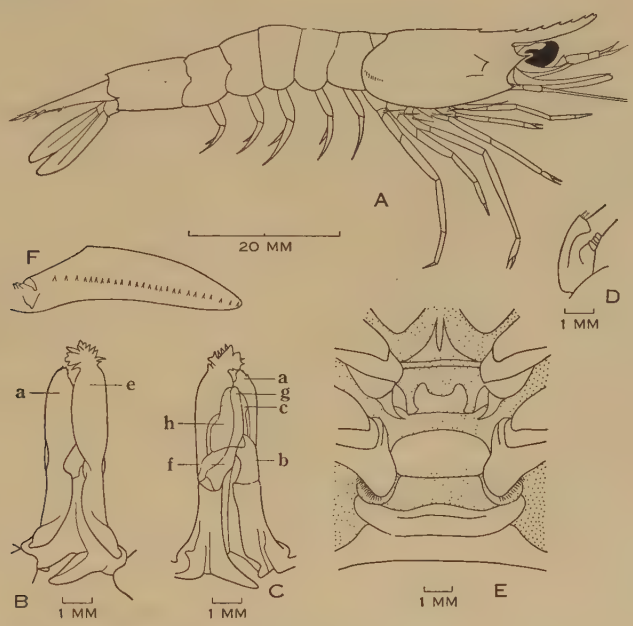

Fig. 11.—*Metapenaeopsis novae-guineae* (Haswell). *A*, 76 mm ♂, Townsville; *B*, ventral surface of petasma; *C*, dorsal surface of same (*a*, right distoventral projection; *b*, right distodorsal lobule; *c*, distomedian lobule; *e*, left distoventral projection; *f*, left distodorsal lobule; *g*, inner intermediate strip; *h*, outer intermediate strip); *D*, appendix masculina, 72 mm ♂; *E*, thelycum, 106 mm ♀; *F*, cardiac plate and zygocardiac ossicle.

Appendix masculina (Fig. 11*D*).—One segment, with cup-like distal expansion bearing a tuft of setae on distal edge.

Thelycum (Fig. 11*E*).—Sternum of 2nd pereiopods with 2 long spinous processes, that of 3rd with 2 shorter blunt projections; genital openings on coxae curved and beak-like. Coxae of 4th pereiopods bounding a very broad plate, ventral edge entire; coxal processes densely setose, posterior edge densely fringed with spinules. Sternum of 5th pereiopods simple, without sharp processes or spines.

Colour and appearance in life.—Carapace and abdomen densely pubescent. Irregularly mottled with dark reddish brown, with transverse band across distal ½ telson and uropods, rostrum and appendages anterior to eyes banded with same colour. Colour between mottling mid brown dorsally, becoming light brown ventrally. Rose pink (Hale 1927).

Distribution

Ranging from Port Jackson, N.S.W., through north and west Australia to south Australia (common in warmer waters). Gulfs of South Australia (Hale 1927). Indonesia, Hong Kong, Gulf of Martaban, coasts of Bay of Bengal to Ceylon (de Man 1911).

Discussion

M. novae-guineae is a variable species, especially in features of the carapace, which in other penaeids are usually constant. Other *Metapenaeopsis* spp. possessing a stridulating organ are *M. barbatus* (de Haan) (= *Penaeopsis akayebi* Rathbun), *M. acclivis* (Rathbun), and *M. durus* Kubo, the first 2 resembling *M. novae-guineae* very closely but readily distinguished by the key characters (see above).

The variability of the species, especially with regard to the petasma, often gives rise to the suspicion that more than one species is being examined, but the thelyca and gastric mills of the specimens from various localities are uniform. A similar difficulty was noted by de Man (1911). The differences between specimens from widely different localities appear greater than those between specimens from the same locality but there do not seem to be any uniform distinctive features that would justify splitting *M. novae-guineae* into 2 or more species.

Schmitt (1926) discusses differences in thelyca between *M. novae-guineae* and *M. mogiensis* (Rathbun). The identity of *Penaeus velutinus* Bate, 1888, has still to be resolved. Bate's Figure 1 (pl. XXXIII) has the stridulating ridge covered by the pleuron of 1st abdominal somite, but telson, stylocerite, petasma, and thelycum (Figs. 1″, 1‴) most nearly resemble those of *M. novae-guineae*. In addition in the Australian Museum there is a specimen of "*Penaeus velutinus*" identified by Bate which is undoubtedly *M. novae-guineae*. There seems little doubt, therefore, that at least the figured specimens of "*Penaeus velutinus*" are *M. novae-guineae*.

Metapenaeopsis mogiensis (Rathbun)

Fig. 12*A*, *B*

Parapenaeus mogiensis Rathbun, 1902, p. 39.
Metapeneus mogiensis Alcock, 1906, pp. 29–30.
Penaeopsis mogiensis Schmitt, 1926, pp. 346–8.
Penaeopsis hilarulus de Man, 1911, pp. 70–1. Barnard, 1950, pp. 595–6.

Material.—QUEENSLAND: Darnley I., Torres Strait (figd. Schmitt 1926), ♀ 32 mm; North West I., Capricorn Group, coll. M. Ward, ♀ 63 mm.

Description

Rostrum.—Teeth 7 + epigastric; rostrum deep, reaching ½ 2nd antennular segment, tip slightly upturned; greatest depth at 2nd tooth. Adrostral carina distinct, reaching postorbital margin of carapace and becoming confluent with it. Postrostral carina absent. Epigastric tooth only on carapace.

Carapace.—Orbital spine small, antennal spine slender, carina absent; cervical sulcus feeble, straight, reaching ½ carapace. Hepatic spine long and slender; hepatic sulcus deep, horizontal below spine, its posterior end slightly upturned; sulcus

curving downwards from base of hepatic spine towards but not reaching branchiostegal border, becoming indistinct at level of pterygostomial spine. Pterygostomial spine short, well above antero-inferior corner of carapace.

Antennules.—Flagella subequal $\frac{1}{2}$ length peduncle. Stylocerite slightly exceeding upper median edge of 1st segment; prosartema slightly exceeding eye. Distomedian spine on 1st segment small but distinct; distolateral spine long, slender, inclined slightly upwards.

Thoracic appendages.—Third maxilliped reaching tip of 2nd antennular segment; 1st pereiopods reaching base, 2nd exceeding tip of carpocerite by dactyl, 3rd reaching $\frac{1}{2}$ 2nd antennular segment, 4th reaching base, 5th exceeding tip of carpocerite by dactyl. (Pereiopods of smaller specimen, where present, longer than those of preceding description by about the dactyl.) Exopods of pereiopods as long as or exceeding the ischia. Ischial spine on 1st pereiopod.

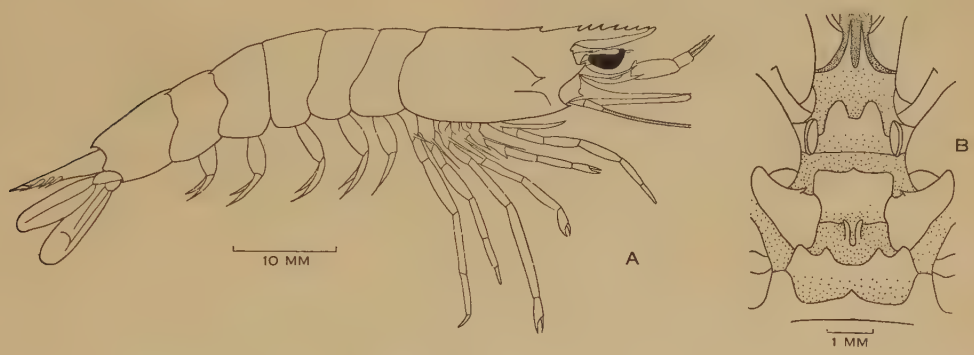

Fig. 12.—*Metapenaeopsis mogiensis* (Rathbun). *A*, 63 mm ♀, North West I.; *B*, thelycum, 63 mm ♀.

Abdomen.—Carina commencing on and bearing sulcus for length 3rd somite; remainder carina non-sulcate and high. Depth 6th somite $\frac{5}{8}$ length. Telson non-sulcate proximally with 3 pairs long movable spines, the most distal pair almost reaching tip of telson, thrice length fixed spines.

Thelycum (Fig. 12*B*).—Sternum of 2nd pereiopods with 2 long spines, 2 blunt processes on 3rd. Transverse plate between 4th pereiopods with median tooth, remainder of anterior border almost straight; width plate $1\frac{1}{2}$ times length. Immediately behind anterior plate a pair of slender divergent tubercles, tending to be more lamellar and less divergent in immature specimen. Anterior 5th sternal ridge with large median and 2 semicircular excavations, the 2 median projections separating them smoothly rounded; these features ill defined in immature ♀. Posterior sternal plate with mucronate median projection.

Distribution and Size

Ranging from Mogi, Japan (type locality), to Capricorn Group, Queensland, and to South Africa (Barnard 1950). Abundant off the Malabar coast, Ceylon, and Andaman Is. (Alcock 1906). Females of 90 mm have been recorded (Alcock 1906).

Discussion

Schmitt (1926), who examined both the type material and the Darnley I. female, could see no reason for regarding de Man's (1911) *P. hilarulus* as a separate species. The only major point of difference is that Rathbun (1902) states that the spines between 2nd pereiopods are rudimentary, whereas de Man shows these spines as well developed. Schmitt, however, states that the spines between 2nd legs (Darnley I. specimen) are like those of a typical *mogiensis* and previously makes reference to a specimen other than the holotype as having the more usual, and possibly less mature type of thelycum. It seems likely that Rathbun's description was taken from an abnormal or damaged specimen. The two major differences between mature and immature thelyca are configuration and size of 2 spines or platelets behind anterior plate of thelycum, and of foremost 5th sternal plate. As the present specimens agree in other features it seems undesirable to separate them. Sexual maturity is apparently reached by ♀♀ at a length of 60–75 mm and a specimen under 40 mm would not show adult secondary sexual features.

The 63 mm ♀ agrees closely with Rathbun's (1902) figures of the rostrum and thelycum, but differs slightly from those of Alcock (1906). Schmitt (1926) noted differences in Alcock's figure of the thelycum compared with Japanese specimens. It is likely there is some variation between adults from various localities.

Metapenaeopsis borradailei (de Man)

Fig. 13*A–E*

Penaeopsis borradailei de Man, 1911, pp. 73–5, pl. VIII, fig. 24*a*, *b*.

Material.—QUEENSLAND: Murray I., Torres Strait (Aust. Mus. regd. No. P7452), ♂ 34 mm.

Description

Rostrum.—Teeth 9 + epigastric, the last minute. Rostrum straight, inclined upwards, reaching tip of 2nd segment of antennular peduncle; epigastric at slightly less than $\frac{1}{4}$ carapace. Adrostral carina reaching almost to 2nd tooth, which is slightly in advance of postorbital margin of carapace; postrostral carina absent.

Carapace.—Densely and harshly pubescent; orbito-antennal sulcus absent; antennal spine large, the carina extending $\frac{1}{4}$ distance between antennal and hepatic spines. Hepatic spine prominent, with distinct but feeble cervical sulcus ascending steeply dorsad, edged with stiff setae. Hepatic sulcus a short horizontal groove immediately below hepatic spine, then turning abruptly ventrad, upper $\frac{1}{2}$ directed anteroventrally, lower $\frac{1}{2}$ descending vertically to edge of branchiostegite; descending portion of sulcus fringed posteriorly with long spinose setae. Pterygostomial spine large.

Antennules.—Upper flagellum shorter than lower, which is $\frac{1}{3}$ peduncle, and $\frac{1}{4}$ length carapace. Prosartema not reaching as far as eye, stylocerite attaining $\frac{2}{5}$ basal segment.

Thoracic appendages.—Third maxilliped reaching middle of 2nd segment of antennular peduncle; 1st pereiopod slightly exceeding carpocerite; 2nd exceeding it by propodus; 3rd reaching tip of 2nd segment of antennular peduncle; 4th reaching

$\frac{1}{2}$ carpocerite. Ischial spine on 1st pereiopod. A pair of long slender spines between coxae of 2nd pereiopods.

Abdomen.—Fifth and 6th somites dorsally carinated; depth 6th somite $\frac{2}{3}$ length. Telson with 3 pairs of lateral movable spines, 1st small, based at $\frac{1}{2}$ length telson, 2nd and 3rd large and close to subapical spine; telson $\frac{4}{5}$ length inner uropod.

Petasma (Fig. 13*B*, *C*).—Right distoventral projection (*a*) large, more or less flap-like; left distoventral projection (*e*) vestigial, its exact limits not clear. Right and left distodorsal lobules large (*b*, *f*). Distomedian lobule (*c*) a bifid structure with minute distal setae. Intermediate strips fused, slender and small (*h*). Petasma reaching basis 3rd pereiopods.

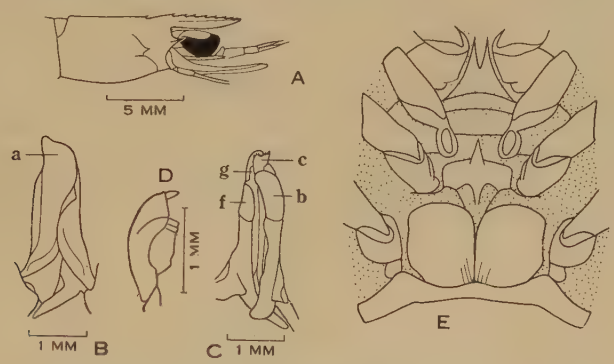

Fig. 13.—*Metapenaeopsis borradailei* (de Man). *A*, cephalothorax, 34 mm ♂; *B*, ventral surface of petasma; *C*, dorsal surface of petasma (*a*, right distoventral projection; *b*, right distodorsal lobule; *c*, distomedian lobule; *f*, left distodorsal lobule; *g*, inner intermediate strip); *D*, appendix masculina (lateral view); *E*, thelycum (after de Man 1911).

Appendix masculina (Fig. 13*D*).—Two-segmented, the distal segment minute, $\frac{1}{8}$ length proximal segment.

Thelycum (Fig. 13*E*; after de Man (1911)).— A single median acute spine situated on transverse plate between coxae 4th pereiopods, this plate united with the posterior thelycum by short median longitudinal ridge. Posterior part with deep median groove, consisting of 2 subrectangular plates, rounded anteriorly with outer surface of each slightly convex. Posterior transverse sternal ridge with 5 or 6 median setae.

Distribution

Murray I., Torres Strait; otherwise known only from the "Siboga" Expedition type localities.

Discussion

The Murray I. specimen is the first record of ♂ of this species, which apart from the distinctive petasma, is readily distinguished from similar species by short stylocerite, hepatic sulcus descending to ventral edge of branchiostegite, and lack of dorsal carination on abdomen anterior to 5th somite. The above description is in

close agreement with that of de Man (1911). It is a small species, the largest specimen recorded by this author measuring "nearly 56 mm". *M. borradailei* is the only species within the genus so far described as possessing a distal segment on appendix masculina.

METAPENAEOPSIS SINUOSUS, sp. nov.

Fig. 14*A–F*

Material.—QUEENSLAND: Off Shore I. (Kennedy Sound), Cumberland Group, trawled 10 fm at night, G. P. Whitley, 5.ix.1935: holotype ♂, 41 mm, carapace 8 mm, Aust. Mus. regd. No. P12223; allotype ♀, 37 mm, carapace 7·8 mm, Aust. Mus. regd. No. P12223.

Diagnosis

Rostrum slender, sigmoidal, and as long as antennular peduncle, with 7 teeth + epigastric; small notch on edge of carapace just above antennal spine; abdomen well developed, length 6th somite more than twice depth measured at posterior end; right lobe of petasma exceeding left; anterior plate of thelycum simple, behind which is a large centrally depressed plate.

Description

Rostrum.—Teeth 7 + epigastric; reaching as far as or slightly exceeding tip of antennular peduncle, slender and sigmoidal, 1st 4–5 teeth long and borne on proximal $\frac{1}{2}$ free portion, remaining 2–3 minute and more widely spaced along distal $\frac{1}{2}$. Epigastric tooth at $\frac{1}{4}$ carapace, 1st tooth in advance of postorbital margin of carapace. Adrostral carina ending at postorbital margin; postrostral carina ending at $\frac{1}{2}$ carapace.

Carapace.—Orbital angle close to rostral base and separated from it by a small depression; a small notch on frontal margin of carapace just above long antennal spine. Orbito-antennal sulcus ill defined; antennal carina absent; cervical sulcus short, not quite reaching $\frac{1}{2}$ carapace. Antennal spine long and slender; hepatic sulcus horizontal, situated immediately below the spine, anterior end level with tip of spine. Pterygostomial spine long.

Eye.—Cornea $\frac{1}{4}$ length carapace; peduncle with triangular scale.

Antennules.—Flagella subequal, $\frac{2}{5}$ length peduncle, $\frac{1}{3}$ length carapace. Prosartema slender, not quite reaching as far as eye; stylocerite reaching $\frac{3}{4}$ basal segment. Spine on inner margin of basal segment small, but fully developed.

Antennae.—Scaphocerite reaching as far as or slightly exceeding antennular peduncle, the spine very slightly exceeding the lamina.

Mandible.—Palp reaching base of carpocerite, distal segment widest at $\frac{1}{2}$ its length, distolateral edge barely concave, making an obtuse angle with the short mediodistal edge. Incisor process a blunt distal tooth separated by a shallow notch from remainder of process. Molar process subrectangular, and flat except for a ridge along the posterior edge.

Maxillule.—Inner margin with basal $\frac{1}{2}$ convex, bearing 4–5 long setae; distal $\frac{1}{2}$ convex, bearing a small spine directed distomedially; apex with small cluster of setae.

Thoracic appendages.—Third maxilliped reaching ½ 2nd segment of antennular peduncle; 1st pereiopod reaching ½ carpocerite, 2nd exceeding it by dactyl, 3rd reaching as far as 3rd maxilliped, 4th almost reaching tip of carpocerite, 5th exceeding it by ½ dactyl. Ischial spine on 1st pereiopod, all exopods minute.

Abdomen.—Dorsally carinated from anterior 3rd somite; carina 6th somite ending in blunt tooth. Length 6th somite 2½ times depth measured at the posterior edge. Telson with 3 pairs lateral movable spines, and slightly shorter than endopod uropod.

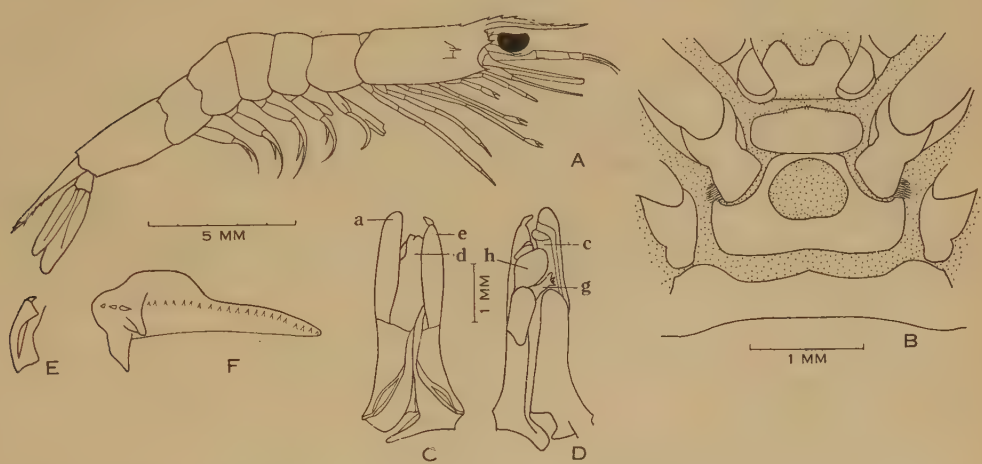

Fig. 14.—*Metapenaeopsis sinuosus*, sp. nov. *A*, 41 mm ♂ (holotype); *B*, thelycum, 37 mm allotype; *C*, ventral surface of petasma of holotype; *D*, dorsal surface of petasma of holotype (*a*, right distoventral projection; *c*, distomedian lobule; *d*, distoventral flap; *e*, left distoventral projection; *g*, inner intermediate strip; *h*, outer intermediate strip); *E*, appendix masculina; *F*, cardiac plate and zygocardiac ossicle of allotype.

Gastric mill (Fig. 14*F*).—Cardiac plate with about 21 spinules. Uppermost tubercle of zygocardiac ossicle with 3–4 teeth on posterior edge, lower with rounded projection on posterior edge. Cardiac ossicle subrectangular; urocardiac bluntly pointed; pterocardiac sigmoidal. Prepyloric with large median tooth, with a smaller tooth on either side ½ length and partially fused with it; distolateral teeth long, spinous, slightly curved, and well separated.

Petasma (Fig. 14*C*, *D*).—Right lobe slightly exceeding left and reaching bases of 2nd pereiopods. Right distoventral projection (*a*), thickened distally and smoothly rounded; left distoventral projection (*e*), with distal inwardly projecting process of irregular shape. Distoventral flap (*d*) large, cylindrical, the apex irregularly truncate; distomedian lobule (*c*) slender, proximally widening towards apex, which is very minutely and densely setose. Inner intermediate strip (*g*) very slender with 3 lateral digitiform processes, outer intermediate strip (*h*) large, lamellar, and subrhomboidal. Posteromedian projection of left proximal piece of petasma much larger than that of right, wide for most of its length, ending in blunt point.

Appendix masculina (Fig. 14*E*).—One-segmented with posterodistal surface oval and excavate, with a small soft process just inside most distal part of rim.

Thelycum (Fig. 14*B*).—A pair of spines on sternum of 2nd pereiopods (absent in ♂); a pair of blunt processes, fringed with setae, on sternum of 3rd pereiopods; a suboval plate, twice as wide as long, with 3 minute spinules on ventral margin, between coxae of 4th pereiopods; behind this plate is a large, centrally depressed plate, widening posteriorly, with posterior edges of 4th coxae each resting in concave anterolateral margin. Posterior transverse sternal plate with obtusely angular median ventral prominence, and 2 convex projections; distolateral corner of the plate sharply angular. Coxae of 4th pereiopods with row of articulate spinules on posterolateral margins.

Discussion

M. sinuosus falls within the group of small slender *Metapenaeopsis* spp. with well-developed abdomen, viz. *M. coniger*, *M. sibogae*, *M. phillippii*, *M. latus*, and *M. kyushuensis*. These species have mostly been recorded at depths greater than 100 m. Apart from the fact that it has been found in relatively shallow water, *M. sinuosus* differs from the above species in having a simple anterior thelycal plate without a posterior process, a doubly recurved rostrum, and only a small spine on the inner margin of the 1st antennal segment.

Genus PARAPENAEUS Smith

Parapenaeus Smith, 1885, p. 170. De Man, 1911, pp. 77–9. Kubo, 1949, pp. 398–9. Barnard, 1950, pp. 600–1.

Parapeneus Alcock, 1901, p. 14; 1906, pp. 32–3.

Rostrum dorsally toothed only. Carapace with longitudinal sutures reaching at least as far as median posterior border of carapace, with transverse sutures just above base of 2nd pereiopods. Cervical, hepatic, and orbito-antennal sulci feeble or absent. Antennal and hepatic spines present, branchiostegal spine often present. Telson with shallow median sulcus and a pair of subapical fixed spines, lateral movable spines absent. First antennular segment with spine on the ventral distomedian border. Maxillulary palp unsegmented. First pereiopod with ischial and basial spines. Minute, barely perceptible exopods on all pereiopods. Petasma open and with apical pair of complex petaloid processes (Fig. 15*B–D*); median lobes thick, often ending in pair of blunt processes (*c*), lateral lobes with lateral process which bifurcates, each part then ending apically in a more or less spinous process (*a* and *b* respectively), process *a* often bearing another small process *d*. Appendix masculina 2 pieces, the proximal with a prominent anterior ridge, the distal irregularly globular. Thelycum with anterior raised plate between coxae of 4th pereiopods, often an intermediate plate which usually has anterior processes embracing posterior part of anterior plate, and a posterior transverse sternal plate. Zygocardiac ossicle consisting of principal tooth + several irregularly disposed smaller teeth. Pleurobranchiae on 3rd to 7th thoracic somites; a rudimentary arthrobranch on 1st, anterior and posterior arthrobranchiae on 2nd to 6th, posterior arthrobranch on 7th thoracic somites; mastigobranchiae on 1st, 2nd, 4th, 5th thoracic somites. Body glabrous.

Type species *P. longirostris* Lucas.

The genus comprises 8 species, all found in relatively deep water. The following key is modified from Kubo (1949) to include *P. australiensis*, sp. nov.

Key to the Species of Parapenaeus

1. Branchiostegal spine present; 5th pereiopods not reaching tip of antennal scale 2
   Branchiostegal spine absent; 5th pereiopods exceeding antennal scale by dactyl ....*P. longipes* Alcock

2(1). Branchiostegal spine on anterior margin of carapace 3
   Branchiostegal spine a little behind anterior margin of carapace 7

3(2). Sixth abdominal somite less than twice length 5th 4
   Sixth abdominal somite a little more than twice length 5th .....*P. americanus* Rathbun

4(3). Process *a* of petasma bifurcate, directed laterally 5
   Process *a* simply pointed, directed distolaterally 6

5(4). Process *b* of petasma long, sharply pointed; process *d* present; thelycum consisting of anterior, intermediate, and posterior plates .....*P. fissurus* (Bate)
   Process *b* short, bluntly pointed; process *d* absent; thelycum consisting of anterior and posterior median bosses and 2 pairs anterior and posterior lateral bosses ....*P. sextuberculatus* Kubo

6(4). Process *d* of petasma well developed; adrostral carina ending just behind 2nd rostral tooth; principal tubercle of zygocardiac ossicle cup-shaped with large number of minute teeth on margin of cardiac plate; longer antennular flagellum shorter than peduncle .. ..*P. australiensis*, sp. nov.
   Process *d* minute, tooth-like; adrostral carina reaching almost to epigastric tooth; principal tubercle of zygocardiac ossicle simple, without minute teeth on margin of cardiac plate; longer antennular flagellum longer than peduncle .....*P. lanceolatus* Kubo

7(2). Rostrum reaching distal end of 1st segment of antennular peduncle; 6th abdominal somite more than twice length 5th .....*P. investigatoris* Alcock
   Rostrum reaching distal end of 2nd segment of antennular peduncle; 6th abdominal somite a little less than twice length 5th .....*P. longirostris* (Lucas)

Parapenaeus australiensis, sp. nov.

Fig. 15*A–F*

Material.—New South Wales: Off Newcastle, Dec. 1953, holotype (Aust. Mus. regd. No. P12329) ♂ 112 mm, carapace 26 mm, and allotype (Aust. Mus. regd. No. P12328) ♀ 114 mm, carapace 29 mm; off Wata Mooli, 68 fm, Apr. 1919, paratypes (Aust. Mus. regd. Nos. P4444–5) 2 ♀ 101, 124 mm.

Diagnosis

Rostrum sigmoidal, teeth 6 + epigastric; postrostral carina sharp, reaching almost to posterior border of carapace. A shallow postocular depression present, branchiostegal spine on anterior margin of carapace. Petasma with 3 processes of lateral lobes (when viewed laterally) each simple and pointed. Thelycum with pear-shaped anterior plate, pointed anteriorly, with intermediate plate with 2 subquadrate lateral processes, and posterior plate with 2 ovoid processes.

Description

Rostrum.—Teeth 6 + epigastric; sigmoidal, in ♂ reaching $\frac{1}{2}$, in ♀ reaching tip of 2nd segment of antennular peduncle. Epigastric at $\frac{1}{3}$ carapace, 2nd tooth just behind anterior margin of carapace; 2nd to 4th teeth fairly widely but evenly spaced, remainder closer together. Adrostral carina ending just behind 2nd rostral tooth. Postrostral carina sharp, ending almost at posterior margin of carapace.

Carapace.—A shallow oval postocular depression at end of adrostral carina; orbital angle sharp. Longitudinal suture ending below posteromedian margin of carapace. Orbito-antennal sulcus distinct for anterior $\frac{1}{3}$ distance between hepatic spine and margin of carapace, a very shallow, barely defined depression marking remainder of distance. Antennal carina occupying $\frac{5}{8}$ distance between hepatic and antennal spines, cervical sulcus short; hepatic sulcus with horizontal, wide, shallow, posterior part, below and behind spine, and anterior part confluent with carina, 2 parts not continuous; hepatic carina curved, commencing well in front of hepatic spine, ending in branchiostegal spine on anterior margin of carapace.

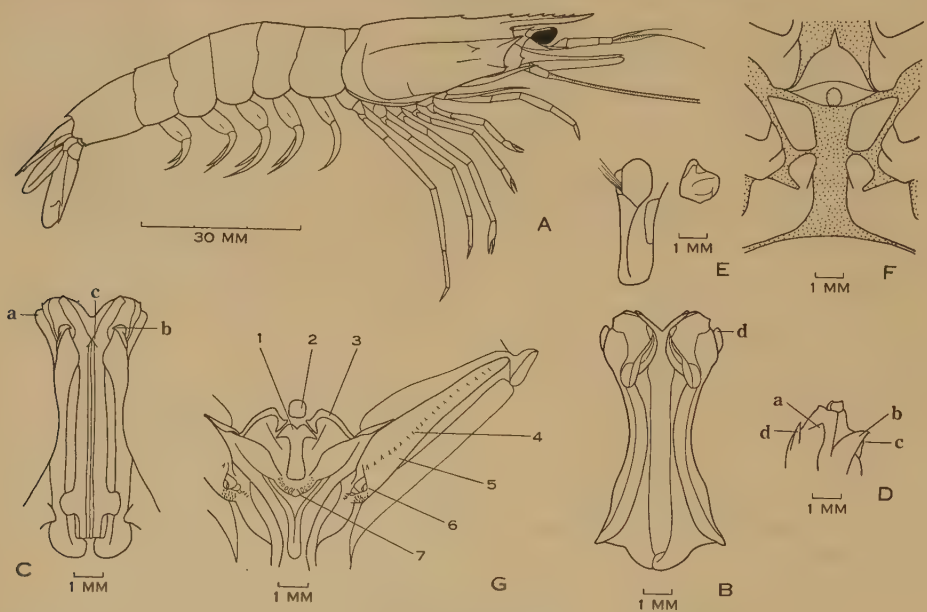

Fig. 15.—*Parapenaeus australiensis*, sp. nov. *A*, allotype; *B*, ventral surface of petasma of holotype; *C*, dorsal surface of petasma; *D*, left lateral distal portion of petasma (*a-c*, spinous processes); *E*, appendix masculina and end view of distal piece; *F*, thelycum of allotype; *G*, inner aspect of gastric mill, cut ventromedially and spread to display the parts: 1, urocardiac ossicle; 2, cardiac ossicle; 3, pterocardiac ossicle; 4, teeth or spinules of cardiac plate; 5, cardiac plate; 6, zygocardiac ossicle; 7, prepyloric ossicle.

Eye.—Proximal segment of ophthalmopod with large acute dorsal scale overlying 2nd segment; longitudinal diameter of cornea equal to $\frac{1}{5}$ carapace.

Antennules.—Second segment of peduncle 0·7 length 1st, 3rd $\frac{1}{2}$ length 2nd. Upper flagellum $\frac{2}{3}$ length lower, which is 0·7 length peduncle. Prosartema reaching as far as eye, stylocerite attaining $\frac{2}{3}$ basal segment.

Antennae.—Basicerite with distolateral spine; scaphocerite slightly exceeding antennular peduncle ♀, reaching $\frac{1}{2}$ 3rd segment in ♂, spine reaching almost as far as lamella; carpocerite reaching below middle cornea.

Mandible.—Palp reaching as far as basicerite, distal segment twice width, with parallel sides, blunt apex, deep but small distolateral excavation; basal segment triangular, length $\frac{1}{2}$ distal segment. Incisor process with deep notch separating distal

and proximal tooth, molar process with large posterior flattened tooth, otherwise flat and of rectangular shape.

Maxillule.—Palp with 2 inner convex flattened setose processes of about equal size, one at $\frac{1}{2}$ segment, the other apical; a proximal rounded densely setose projection on outer side. Anterior face of palp with diagonal row of long setae commencing at outer base and running to apex.

Thoracic appendages.—Third maxilliped reaching $\frac{2}{3}$ 2nd segment of antennular peduncle; 1st pereiopod reaching $\frac{1}{2}$ carpocerite; 2nd reaching tip of carpocerite; 3rd reaching 2nd segment of antennular peduncle; 4th and 5th reaching as far as 1st segment of peduncle.

Abdomen.—Third somite bluntly angular dorsally, sharp dorsal carina beginning at anterior 4th somite, ending on each of 4th, 5th, 6th somites in a horizontal tooth, that of 5th larger than 4th, that of 6th larger than 5th. Spines of telson with bases at $\frac{4}{5}$ length telson. Median sulcus of telson shallow posteriorly, fading out at level of subapical spines. Basis and exopod uropods each with minute distolateral spine.

Gastric mill (Fig. 15*G*).—Cardiac plate with 20–25 spinules. Zygocardiac ossicle a large complex principal tubercle, an irregular row of 3–5 long teeth, and on lower edge of cardiac plate a series of irregular rows of minute teeth; principal tubercle cup-shaped, formed by incomplete fusion of 4 teeth. Cardiac ossicle ovoid; urocardiac with 2 lateral, slightly recurved, wing-like processes; pterocardiac strongly arched. Prepyloric ossicle with rounded rim, median tooth, 4–6 long rounded lateral teeth projecting at right angles to flat surface of ossicle.

Petasma (Fig. 15*B*, *C*).—Apical lobes rosebud-like. Lateral processes dividing near base of petasma, dorsal process ending in a slightly recurved distal spine (*b*); ventral process divides into mediodistal spinous process (*a*), and ventral spinous process (*d*). Median lobe with 2 blunt distal tubercles (*c*), and 2 expanded wing-like processes towards proximal end. Apex petasma reaching coxae of 4th pereiopods, maximum width $\frac{1}{2}$ total length.

Appendix masculina (Fig. 15*E*).—Distal piece rounded, $\frac{1}{2}$ length basal piece and with median groove bearing a small tuft of setae. Posterodistal surface convoluted.

Thelycum (Fig. 15*F*).—Anterior plate pear-shaped, anterior end sharp, posterior with small depression. Intermediate plate with 2 raised processes on either side of wide median groove; posterior sternal plate continuous with this groove, and with 2 ovoid anterior processes on either side of groove.

Discussion

P. australiensis belongs to the closely related group of *Parapenaeus* spp. with a branchiostegal spine on the anterior border of the carapace. *P. fissurus* (Bate) and *P. sextuberculatus* Kubo both possess a bifurcate median lateral process of the petasma, and the anterior plate of the thelycum is not sharp anteriorly. *P. lanceolatus* Kubo, of which the female is unknown, is the most closely similar to the present sp. As Kubo's description is sketchy and relies mainly on petasmal features, the key characters are the best available for separation of the 2 species. In addition *P. australiensis* is almost twice the length of *P. lanceolatus* at maturity.

Genus METAPENAEUS Wood-Mason & Alcock

Metapenaeus Wood-Mason and Alcock, 1891, p. 271. Burkenroad, 1934*b*, pp. 4, 29. Kubo, 1949, pp. 327–8. Barnard, 1950, pp. 596–7.
Metapeneus Alcock, 1906 (part), p. 16.
Penaeopsis de Man, 1911 (part), pp. 53–5, 61. Schmitt, 1926 (part), pp. 319–23.

Rostrum dorsally toothed only. Carapace without longitudinal or transverse sutures, orbital angle usually sharp. Postocular sulcus present, cervical sulcus well defined. Hepatic sulcus not well defined or absent behind level of hepatic spine, but pronounced in front with a well-defined postero-inferior border, usually descending vertically from hepatic spine, then turning towards the pterygostomial angle. Antennal and hepatic spines pronounced. Pterygostomial angle blunt. Telson with deep dorsomedian sulcus, without fixed subapical spines, and with movable dorsolateral spines which may be microscopic and very numerous. First antennular segment without spine on ventral distomedian border. Antennular flagella shorter than carapace. Maxillulary palp with 2 segments, distal small, basal with convex, foliaceous projections on inner and outer edges, and a long spine on inner edge. First to 3rd pereiopods with basial spines, no exopod on 5th. Ischium and merus of 5th pereiopod often modified in adult ♂. Petasma tubular with thickened median lobes; lateral lobes thicker than median, forming distolateral spout-like projections, each with a dorsal lobule produced posteriorly into an expanded, plate-like projection; median lobes with dorsal lobule produced into a thin recurved, plate-like, or hood-like structure. Appendix masculina with a knob-like distal piece which bears either a deep posterodistal depression or is sculptured in some way. Thelycum composed of anterior median plate and 2 posterior lateral plates more or less enclosing posterior end of median plate; posterior plates often continuous across sternite. Zygocardiac ossicle with 2 rows of teeth which get progressively smaller. Pleurobranchiae on 3rd to 7th thoracic somites, a rudimentary arthrobranch on 1st, anterior and posterior arthrobranchiae on 2nd to 6th, and an anterior vestigial and a posterior fully developed arthrobranch on 7th thoracic somites; mastigobranchiae on 1st, 2nd, 4th–6th thoracic somites. Body usually with at least a few dorsal setose depressed areas, remainder of body surface varying from being completely glabrous to covered with close irregular setose depressed areas.

Burkenroad (1934*a*) restricted the definition of the genus to separate the species enumerated below from those with a branchiostegal spine and fixed subapical spines on the telson, which he included in the genus *Penaeopsis* Bate. Hitherto, *Metapenaeus* and *Penaeopsis* had been regarded as synonymous (*Penaeopsis* has been further restricted by Kubo (1949); see *Metapenaeopsis*).

The following well-established species are included in the genus *Metapenaeus*: type species *M. affinis* (Milne Edwards); *M. monoceros* (Fabricius); *M. intermedius* (Kishinouye); *M. endeavouri* (Schmitt); *M. mastersii* (Haswell); *M. burkenroadi* Kubo; *M. eboracensis*, sp. nov.; *M. demani* (Roux); *M. dobsoni* (Miers); *M. joyneri* (Miers); *M. tenuipes* Kubo; *M. lysianassa* (de Man); *M. stebbingi* (Nobili); *M. brevicornis* (Milne Edwards); *M. spinulatus* Kubo; *M. macleayi* (Haswell).

Burkenroad (1934*a*) regards *Penaeopsis elegans* de Man, 1911, *Penaeus incisipes* Bate, 1888, *Metapenaeus deschampi* Nobili, 1903, *M. cognatus* Nobili, 1906, and

Penaeopsis spinulicauda Stebbing, 1914, as being immature specimens of *M. monoceros*, but for the present they are better regarded as doubtful species. It is likely that *Penaeus mutatus* Lanchester, 1901, is synonymous with *Metapenaeus affinis* as Burkenroad (1934*a*) suggests. *M. ensis* (de Haan) is a nomen nudum, the cephalothorax being that of *M. monoceros* and the abdomen that of a *Metapenaeopsis* sp. (L. B. Holthuis, personal communication).

Many members of this genus, especially the more pubescent species with minute spinules on the telson, are closely similar in general appearance and have been confused in the past. The following key to the genus as defined by Burkenroad (1934*a*) does not include the above doubtful species.

Key to the Species of Metapenaeus

1. Abdomen with a number of pubescent depressed areas 2
   Abdomen uniformly glabrous 14

2(1). Ischial spine on 1st pereiopod 3
   Ischial spine absent on 1st pereiopod 5

3(2). Ischial spine much smaller than basial spine; branchiocardiac carina present; 2nd and 3rd abdominal somites with dorsal carina ..... *M. monoceros* (Fabricius) (=*M. incisipes* (Bate))
   Ischial spine subequal to basial spine; branchiocardiac carina absent or merely a flat glabrous strip marking its position; 2nd and 3rd abdominal somites without distinct dorsal carina 4

4(3). Branchial region with small pubescent areas; thelycum with median boss close to posterior edge of last thoracic sternite ..... *M. intermedius* (Kishinouye)
   Branchial region with 2 large pubescent areas; no median boss on last thoracic sternite in ♀ ..... *M. endeavouri* (Schmitt)

5(2). Rostrum exceeding distal end of basal segment of antennular peduncle 6
   Rostrum short, not reaching distal end of basal segment of antennular peduncle ..... *M. lysianassa* (de Man)

6(5). Carpocerite reaching below middle cornea; petasma with hood- or spout-like distomedian projections 7
   Carpocerite reaching at least as far as the eye; petasma with slender or with simple flap-like median projections 8

7(6). Gastrofrontal sulcus well defined and glabrous; cardiac plate with 26–32 spinules; distomedian projections of petasma retort-shaped ..... *M. mastersii* (Haswell)
   Gastrofrontal sulcus not a well-defined glabrous region; cardiac plate with 32–35 spinules; distomedian projections of petasma hood-like ..... *M. burkenroadi* Kubo

8(6). Distomedian projections of petasma simple, flap-like 9
   Distomedian projections of petasma slender 12

9(8). Basial spine of 3rd pereiopods in adult ♂ long, barbed; 2 tubercles on merus of ♂ 5th pereiopod ..... *M. dobsoni* (Miers)
   Basial spine of 3rd pereiopods in adult ♂ simple; 1 tubercle on merus of ♂ 5th pereiopod 10

10(9). Thelycum with flat leaf-like anterior plate 11
   Thelycum with tongue-like anterior plate, grooved longitudinally and with 2 rounded anterior projections ..... *M. affinis* (Milne Edwards)

11(10). Anterior plate of thelycum with blunt point directed forwards; posterior plate flat except for median fissure ..... *M. eboracensis*, sp. nov.
   Anterior plate of thelycum broad and with smoothly rounded anterior margin; posterior plate forming a cup-shaped depression ..... *M. demani* (Roux)

12(8). Postrostral carina absent or very feeble; distomedian projections of petasma straight, each with serrate border ..... *M. stebbingi* (Nobili)
Postrostral carina well defined; distomedian projections of petasma recurved posteriorly, borders not serrate 13

13(12). Postrostral carina reaching $\frac{8}{9}$ carapace; 1st–6th abdominal somites dorsally carinated ..... *M. joyneri* (Miers)
Postrostral carina reaching middle of carapace; 1st–3rd abdominal somites without dorsal carina ..... *M. tenuipes* Kubo

14(1). Telson with large mobile lateral spinules; median plate of thelycum smaller than posterior plates 15
Telson not conspicuously armed; median plate of thelycum larger than posterior plates ..... *M. brevicornis* (Milne Edwards)

15(14). Telson with 2 pairs lateral spines; posterior plate of thelycum not enclosing prominent rounded tubercles ..... *M. spinulatus* Kubo
Telson with 4 pairs lateral spines; posterior plate of thelycum enclosing 2 prominent rounded tubercles ..... *M. macleayi* (Haswell)

Metapenaeus monoceros (Fabricius)

Fig. 16*A–H*

Penaeus monoceros Fabricius, 1798, p. 409.
Metapeneus monoceros Alcock, 1906, pp. 18–20.
Metapenaeus monoceros Burkenroad, 1934*a*, pp. 32–3. Kubo, 1949, pp. 329–33. Barnard, 1950, pp. 597–9.
Penaeopsis monoceros de Man, 1911, pp. 55–7. Schmitt, 1926, pp. 325–9 (not incl. "*Penaeus mastersii*").
Penaeus incisipes Bate, 1888, pp. 257–8, pl. 34, figs. 2, 2″ (not including female). Kishinouye, 1900, pp. 18–19.
Metapenaeus incisipes Racek, 1955, pp. 230–2.

Material.—QUEENSLAND: F.I.S. *Endeavour* specimens (Aust. Mus. coll.); Moreton Bay, Townsville, 12 specimens, 68–149 mm. NEW SOUTH WALES: Broadwater (coll. A. A. Racek), ♂ 139 mm. WESTERN AUSTRALIA: Exmouth Gulf, ♂ 105 mm; Australian Museum collection.

Description

Rostrum.—Teeth 8–10 + epigastric; varying in shape, sometimes slightly depressed apically but usually projecting upwards slightly with ventral upward curve reaching to or almost to tip of antennular peduncle. Adrostral carina ending between epigastric and 1st tooth, sulcus extending behind epigastric, reaching $\frac{1}{3}$–$\frac{1}{2}$ carapace. Postrostral carina distinct, continuing to posterior border of carapace.

Carapace.—Postocular sulcus at angle of about 40° to rostrum. Orbito-antennal sulcus wide, shallow, meeting hepatic below hepatic spine. Hepatic sulcus descending vertically for upper $\frac{1}{3}$, then curving towards pterygostomial angle. Cervical sulcus straight, ending at 0·3–0·4 length carapace. Epigastric spine at $\frac{1}{4}$ carapace. Branchiocardiac sulcus indistinct, carina distinct and meeting glabrous posterior extension of hepatic spine.

Antennules.—Flagella subequal $\frac{1}{2}$ length peduncle. Prosartema exceeding eye, but not reaching tip of basal segment, stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Third maxilliped and 1st pereiopod reaching $\frac{3}{4}$ carpocerite; 2nd pereiopod reaching tip of 1st segment, 3rd reaching to or beyond tip of

2nd segment of antennular peduncle; 4th reaching tip of carpocerite; 5th reaching at least middle 2nd segment of antennular peduncle in ♂, and reaching its base in ♀. A small blunt ischial spine on 1st pereiopod. A large triangular distoventral keel on ischium of 5th pereiopod in mature ♂, followed by a deep notch on merus, bounded by a prominent spinous process twisted ventrally at angle 90° to axis of merus, usually followed by a ventral row of conical tubercles, which end in a small keel at distal $\frac{1}{4}$ merus; tubercles sometimes reduced or absent.

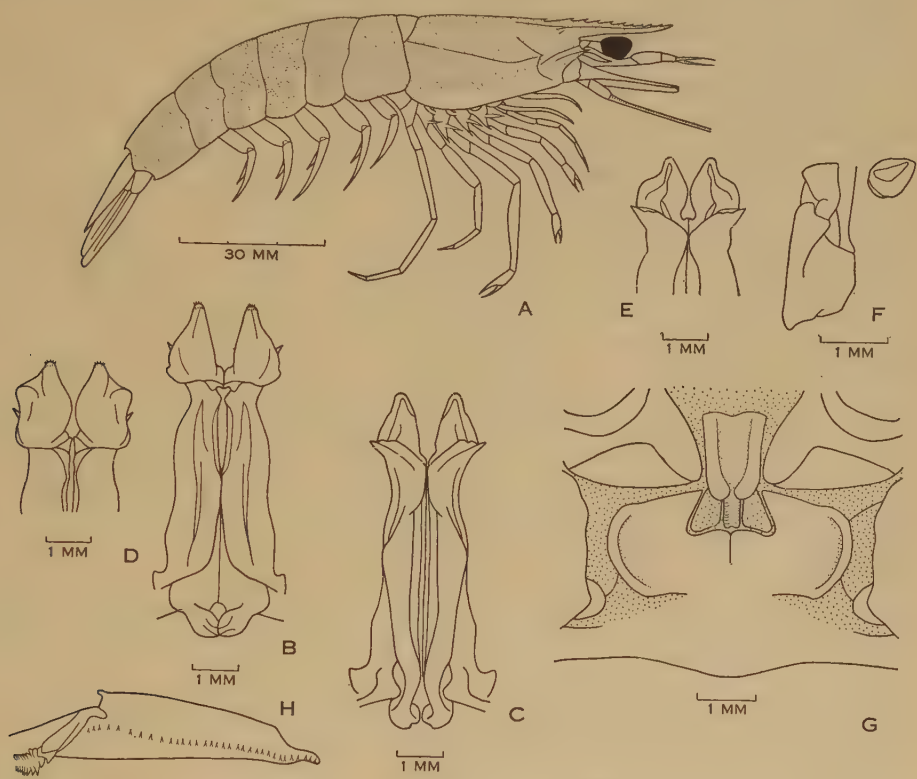

Fig. 16.—*Metapenaeus monoceros* (Fabricius). *A*, 138 mm ♀; *B*, ventral surface of petasma, 138 mm ♂; *C*, dorsal surface of petasma; *D*, *E*, distal ventral and dorsal surfaces respectively of petasma, 130 mm ♂; *F*, appendix masculina and end view of distal piece, 138 mm ♂; *G*, thelycum, 138 mm ♀; *H*, cardiac plate and zygocardiac ossicle.

Abdomen.—Traces of dorsal carina usually present on 1st somite, becoming progressively more prominent to 6th. Telson with 3 or 4 rows minute dorsolateral spinules on distal $\frac{1}{2}$. Exopod uropod with outer proximal depression in ♂.

Gastric mill (Fig. 16*H*).—Cardiac plate with 28–36 spinules. Zygocardiac ossicle with upper row of 8–9 short tubercles of which 1st 3 are usually blunt, remainder more spinous, and a lower row of 9–12 longer tubercles, 1st 2 relatively blunt, remainder spinous. Prepyloric ossicle with rounded median tubercle with 4–5 blunt lateral tubercles and 1 or 2 small spines, usually at an angle to tubercles.

Petasma (Fig. 16*B–E*).—Apex of petasma barely reaching bases of 2nd pereiopods. Distomedian projections $\frac{1}{4}$ total length petasma, overlying distolateral projections, with openings facing dorsolaterally; openings closed by convex flap on distoventral edge of opening; this flap sometimes flat and projecting laterally, when distomedian projections appear quadrangular, sometimes reflected back, when projections appear triangular. Apices of projections with 1 or 2 rows minute setae. Distolateral projections spout-like with large distal openings; distance between projections $\frac{1}{3}$ total length petasma.

Appendix masculina (Fig. 16*F*).—Distal piece with flattened apex 0·7–0·8 length basal piece, posterior depression a very elongate pear shape with narrow part at obtuse angle to broad part.

Thelycum (Fig. 16*G*).—Anterior plate level with and bounded on either side by expanded coxal projections of 4th pereiopods; with median groove deepening posteriorly, between 2 projecting carinae (rounded when viewed laterally). Posterior plates strongly concave, middle part much above ventral surface of anterior plate, lateral edge level with it; anterior part with angular projections facing inwards under anterior plate, enclosing 2 flat plates lying on either side of posterior tongue-like extension of anterior plate; the whole having a cup-shaped appearance, but open posteriorly.

Colour in life.—Body irregularly pubescent. Light tan or pink to brown; pleopods, uropods, and antennae red; peduncles of pleopods and tips of uropods purple; ischia and mera of pereiopods striped orange and cream. Pale, more or less semitransparent with bluish speckling, chiefly in the form of crossbands on abdominal segments, flagellum of antennae reddish, pleopods bluish (Barnard 1950).

Distribution

Ranging from northern New South Wales (Racek 1955) to Exmouth Gulf, W.A.; through Indonesia and Philippine Is. to southern Japan (Kubo 1949); through Indian seas to Red Sea and Mediterranean (by migration through Suez Canal); Mauritius and south-eastern South Africa. Mature adults are usually taken in water of at least 10 fm depth, often much deeper (cf. *M. mastersii*).

Discussion

There are a number of minor discrepancies in descriptions of specimens of this species from various localities, especially those of the median projections of the petasma. This apparently very widely ranging species may be a complex of closely related species differing only in minute characters, but at present there is not sufficient evidence to support this. All descriptions of carapaces and thelyca seem to be in agreement. The median projections of the petasma vary even in specimens collected from the same locality. Of the *Endeavour* specimens E.6612, 130 mm ♂, has a petasma with subrectangular apical projections, which lie close together (Fig. 16*D*, *E*); E.6614 (122 mm), E.6616 (123 mm), have similar apices but with a wider space between them; E.6614, 124 and 130 mm, have the distolateral flaps reflected back, giving the apices a triangular appearance. The petasmas figured by de Man (1911), and by Kubo (1949), could well be those of the Australian species. As apices of the petasmas of this species vary considerably, use of details of this structure

alone for specific identification is undesirable. The few colour descriptions in the literature are also at variance. The coloured plate of Kishinouye (1900) agrees with the above and Racek's (1955) description. Except for antennal flagellae and pleopods, Barnard's (1950) description is quite different from these. It is possible that the species is subject to more than the usual colour variations.

Racek (1955) has identified his specimens, together with those of Kishinouye (1900), as *M. incisipes* (Bate), mainly on the basis of colour and apical projections of the petasma. Mr. J. C. Yaldwyn (personal communication) compared Bate's type specimen in the British Museum with Racek's photographs, and could find no major differences. The identity of the Australian specimens and Bate's "*Penaeus incisipes*" is established, and it remains to decide whether they are identical with *M. monoceros* (Fabricius). Reasons for separation seem insufficient at present, and until further work has been done, it is best to regard the Australian specimens as *M. monoceros*.

The following features, apart from the distinctive petasmas and thelyca, are useful for distinguishing *M. monoceros* from *M. mastersii* (see discussion under the latter species):

Feature	*M. monoceros*	*M. mastersii*
Gastrofrontal sulcus	Absent	Present
Adrostral sulcus	Reaching $\frac{1}{3}$ to $\frac{1}{2}$ carapace	Barely extending behind epigastric tooth
Branchiocardiac carina	Present, extending almost to hepatic spine	Absent
Postrostral carina	Reaching posterior margin of carapace, always distinct	Ending before posterior margin of carapace, always low, and often indistinct
Ischial spine on 1st pereiopod	Small blunt spine present	Spine absent, but a blunt angle persists

METAPENAEUS ENDEAVOURI (Schmitt)

Fig. 17*A–F*

Penaeopsis endeavouri Schmitt, 1926, pp. 329–33, pl. LIX, figs. 1–3, pl. LXVIII, fig. 4.
Metapenaeus endeavouri Kubo, 1949, pp. 339–40. Racek, 1955, pp. 229–30.

Material.—Moreton Bay, Qld., to Shark Bay, W.A., 13 specimens, 111–143 mm; numerous specimens trawled from Exmouth Gulf; Australian Museum collection.

Description

Rostrum.—9–10 teeth + epigastric; of obtuse triangular shape, free portion inclined upwards from carapace, length 4 times depth; reaching from proximal to distal end of 3rd segment of antennular peduncle. Adrostral carina ending behind 2nd tooth, sulcus ending behind epigastric. Postrostral carina distinct, ending in

a glabrous expansion $\frac{1}{9}$ length carapace from its posterior edge, 3rd spine at margin of carapace.

Carapace.—Postocular sulcus at angle of 45° to rostrum, $\frac{1}{7}$ length carapace. Orbito-antennal sulcus narrow, well defined, meeting hepatic below hepatic spine. Antennal carina distinct for $\frac{3}{4}$ distance between antennal and hepatic spines. Hepatic sulcus descending vertically for $\frac{1}{2}$ its length, then curving towards pterygostomial angle, extremity almost horizontal. Cervical sulcus straight, ending at 0·45 length carapace. A feeble accessory cervical sulcus running from below level of hepatic spine, more or less parallel to cervical sulcus but with a break in its lower $\frac{1}{3}$ and reaching further dorsally than cervical sulcus. Branchiocardiac sulcus present, bounded on either side by a glabrous strip, an appreciable carina absent. Sulcus reaching almost $\frac{1}{2}$ carapace.

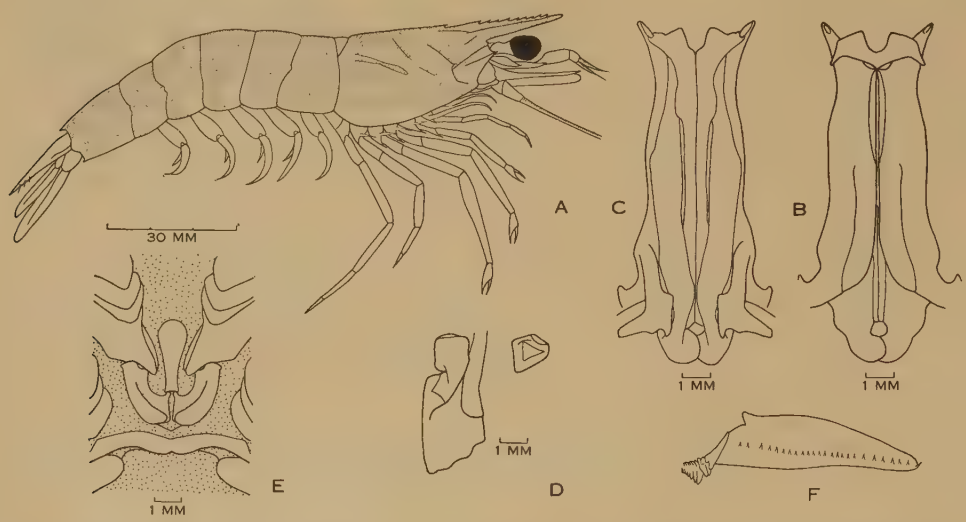

Fig. 17.—*Metapenaeus endeavouri* (Schmitt). *A*, 136 mm ♀; *B*, ventral surface of petasma, 121 mm ♂; *C*, dorsal surface of petasma; *D*, appendix masculina and end view of distal piece; *E*, thelycum, 134 mm ♀; *F*, cardiac plate and zygocardiac ossicle.

Antennules.—Flagella subequal, $\frac{1}{2}$ length peduncle in ♂, $\frac{2}{5}$ in ♀. Prosartema reaching as far as eye, stylocerite attaining $\frac{1}{2}$ basal segment antennular peduncle.

Thoracic appendages.—Third maxilliped and 1st pereiopod reaching as far as or slightly exceeding carpocerite; 2nd pereiopod reaching from base to $\frac{1}{2}$ 2nd segment of antennular peduncle; 3rd reaching tip of antennular peduncle or exceeding it by dactyl; 4th ranging from base to tip of carpocerite; 5th ranging from base to tip of 2nd segment of antennular peduncle. A large ischial spine on 1st pereiopod. Ischium of 5th pereiopod in adult ♂ with low ventral keel, merus with proximal notch followed by keel-shaped tubercle.

Abdomen.—First to 3rd abdominal somites with median dorsal glabrous strips, carina discernible from posterior $\frac{1}{2}$ of 4th somite. Telson with 3 pairs large movable spines, becoming progressively larger distally.

Gastric mill (Fig. 17*F*).—Cardiac plate with 24–30 spinules. Zygocardiac ossicle with upper row 9–11 short tubercles, and lower row 2 large rounded tubercles, at an angle and well separated from remaining 7–10 long tubercles; in advance of latter on edge of cardiac plate 2–3 small spines; prepyloric ossicle with 8–9 lateral tubercles + median rounded tubercle.

Petasma (Fig. 17*B*, *C*).—Apex reaching $\frac{1}{2}$ bases 3rd pereiopods. Median projections triangular flaps closing distal end of petasma, apices of flaps almost level with distolateral projections; lateral corners flaps with tongue-like projections slightly exceeding lateral margins of petasma. Lateral lobes with pointed distolateral projections, distance between their tips $\frac{3}{8}$ length petasma.

Appendix masculina (Fig. 17*D*).—Distal piece 0·7 length basal piece, and with small triangular posterior depression.

Thelycum (Fig. 17*E*).—Anterior plate rounded anteriorly, concave, tapering posteriorly; ventral surface above coxal expansions of 4th pereiopods; coxal expansions tapering posteromedially to blunt points. Seminal receptacle with deep median fissure separating 2 posterior blunt keel-like tubercles on posterior edge; anterior part on either side produced into blunt process overlying coxal projections of 4th pereiopods, and enclosing 2 oval plates. Sternal plate of 5th pereiopods rounded transversely, ventral edge lower than that of seminal receptacle.

Colour in life.—Body generally light brown, sometimes reddish; antennae and borders of antennal scale bright red; ophthalmopods yellowish green, corneas speckled black; rostrum, postrostrum, and abdominal carina dark brown; uropods and telson light brown proximally, changing to yellow-green and becoming brilliant blue distally; fringing setae reddish brown; pereiopods yellow proximally, white distally, sometimes pink; pleopods with white areas on peduncles, rami yellow.

Distribution

Moreton Bay, Qld., to Shark Bay, W.A.

Discussion

Schmitt (1926) gives a detailed account of the differences between the present species and *M. intermedius* (Kishinouye). The following features are useful for differentiation of *M. endeavouri* from *M. intermedius*:

Feature	*M. endeavouri*	*M. intermedius*
Distomedian projections of petasma	Not reaching as far as distolateral horns	Reaching as far as distolateral horns
Appendix masculina	Triangular	Elongate pear shape
Thelycum	No median boss on posterior sternite	Median boss present on posterior sternite
Cardiac plate	24–30 spinules	40–43 spinules

METAPENAEUS MASTERSII (Haswell)

Greentail, River, or Greasy-back Prawn, eastern Australia; School Prawn, Western Australia

Fig. 18*A–G*

Penaeus mastersii Haswell, 1879, p. 42; 1882, p. 203.
Penaeus sp. Whitelegge, 1890, p. 225. Whitelegge, in Ogilby, 1893, p. 203.
Penaeopsis monoceros Schmitt, 1926, pp. 325–9, pl. LVIII, figs. 1, 2 ("*Penaeus mastersii*" only; not incl. *Endeavour* material).
Penaeopsis affinis de Man, 1911, pp. 57–8.
Metapenaeus, sp. nov.; Morris and Bennett, 1952, pp. 164–82 (life-history and larval development).
Metapenaeus mastersii Racek, 1955, pp. 232–5.

Material.—QUEENSLAND: Moreton Bay, Brisbane River, numerous specimens, 6–104 mm. NEW SOUTH WALES: Tuggerah Lakes, 27 specimens. WESTERN AUSTRALIA: Swan River to Exmouth Gulf, 28 specimens. Australian Museum collection.

Description

Rostrum.—Teeth 7–8 + epigastric; slender with slight upward curve, usually reaching tip of 2nd segment of antennular peduncle in ♂, reaching to or beyond tip of peduncle ♀, tip sometimes slightly malformed. Adrostral carina ending between epigastric and 1st tooth, sulcus continuing to just beyond epigastric. Postrostral carina variable, distinct but not prominent, glabrous to $\frac{1}{2}$ distance between epigastric tooth and edge of carapace, where it widens and becomes confluent with other irregular glabrous regions of carapace; posterior $\frac{1}{2}$ sometimes continuing as a relatively narrow glabrous strip to $\frac{1}{10}$ length carapace from its posterior edge, where it again becomes confluent laterally with other glabrous areas; sometimes widening and losing its identity as it approaches posterior edge of carapace (Swan River specimens).

Carapace.—Gastrofrontal sulcus present, very wide and shallow without a carina, continuous posteriorly with postocular sulcus, which runs at angle of 45° to rostrum. Orbito-antennal sulcus narrow posteriorly and ending in front of hepatic spine. Cervical sulcus straight and ending at $\frac{1}{2}$ carapace. Epigastric spine at $\frac{1}{4}$ length carapace. Hepatic sulcus descending vertically for $\frac{1}{3}$ length, remainder inclined at an angle towards pterygostomial angle. Branchiocardiac sulcus feeble, anterior end not exceeding the posterior $\frac{1}{3}$ carapace, carina absent.

Antennules.—Flagella equal in length and about $\frac{1}{2}$ length peduncle. Prosartema reaching almost as far as eye, stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Third maxilliped reaching tip of carpocerite; 1st pereiopod reaching $\frac{1}{2}$ carpocerite; 2nd reaching as far as eye; 3rd almost reaching tip of 2nd segment of antennular peduncle; 4th reaching as far as 1st; 5th reaching from base to tip of dactyl of 3rd pereiopod. A small blunt angle on ischium 1st pereiopod. Merus of 5th pereiopod ♂ with deep notch and blunt tubercle, slightly inclined upwards; a small ventral ischial keel.

Abdomen.—Dorsally carinated from anterior 4th somite, but in more pubescent specimens a narrow glabrous region on 2nd and 3rd somites. Telson fringed with numerous minute spines. Exopod ♂ uropod with an outer proximal depression.

Gastric mill (Fig. 18*G*).—Cardiac plate with 26–32, usually 28 spinules. Zygocardiac ossicle with upper row of 7–8 short blunt spines, 1st 3 often flat-topped tubercles, and lower row of 10–12 longer spines, 1st 2 blunter than remainder; 2 small spines on edge of cardiac plate. Prepyloric ossicle with rounded median tubercle and 5–7 blunt lateral tubercles, followed by 2–3 minute spines.

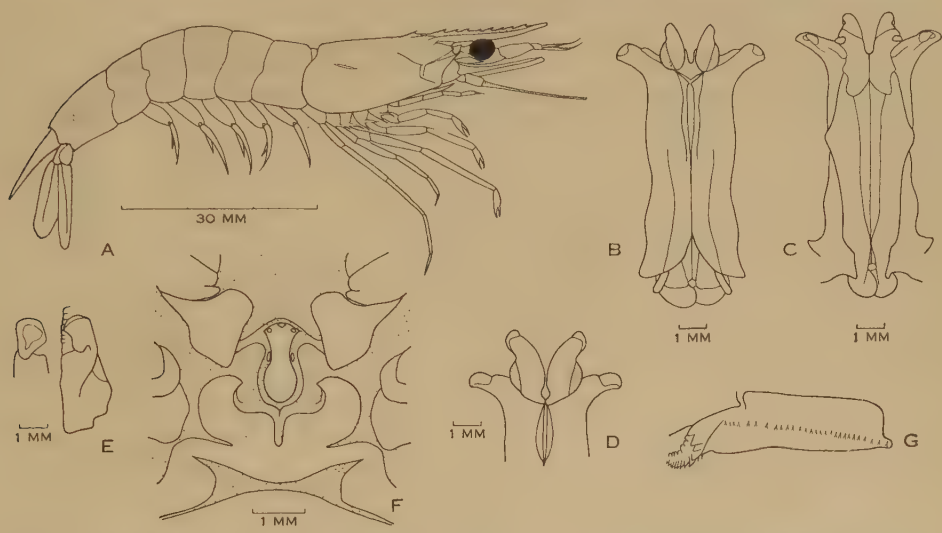

Fig. 18.—*Metapenaeus mastersii* (Haswell). *A*, 92 mm ♀; *B*, ventral surface of petasma, 104 mm ♂; *C*, dorsal surface of same; *D*, distal ventral surface of petasma, 80 mm ♂ from Swan River; *E*, appendix masculina and end view of distal piece; *F*, thelycum, 92 mm ♀; *G*, cardiac plate and zygocardiac ossicle.

Petasma (Fig. 18*B–D*).—Reaching lower $\frac{1}{2}$–$\frac{1}{3}$ basis of 3rd pereiopod. Distomedian projections spout-like and tapering $\frac{1}{4}$–$\frac{1}{5}$ total length petasma, inner edges convex and diverging, posteroventral edge with hemispherical minutely pitted projection, anterodorsal edge with an inwardly projecting convolution apparently dividing lateral aperture; position and extent of convolution varying, influencing extent to which anterodorsal edge projects beyond posteroventral edge. Distolateral projections spout-like with spatulate tips, distance between tips $\frac{1}{2}$ length petasma.

Appendix masculina (Fig. 18*E*).—Distal piece subspherical, almost equal length basal piece, and with posterior pear-shaped depression.

Thelycum (Fig. 18*F*).—Anterior plate with 5 tubercles, 2 anterolateral and conical on either side of an anteromedian triangular tubercle, and 2 blunt lateral tubercles which lie on either side of an elongate flask-shaped sulcus with "neck" anterior to "bulb". Seminal receptacle slightly concave laterally, otherwise flat with median fissure, width slightly more than twice length. Lateral part hooked, tip of hook facing inwards. Coxa of 5th leg with small tuft of setae; coxa of 4th leg and hooks of seminal receptacle with dense tufts of setae overlying anterior plate.

Colour in life.—Body irregularly pubescent, the extent and number of these areas varying with age and locality; semitransparent, speckled with dark brown; tips of uropods, pleopods, and antennal scales green.

Distribution

Ranging from Port Hacking, N.S.W., northwards to Swan River, W.A., Djangkar (Java), Lombok, Bay of Bima, Saleyer anchorage (de Man 1911). Found principally in estuaries and very shallow coastal waters, commercially important in Australia. Spawning takes place in coastal lakes or coastal waters of about 3–5 fm (Morris and Bennett 1952; Dall, unpublished data).

Discussion

Metapenaeus mastersii has previously been confused with *M. monoceros*, although Whitelegge (1890) regarded it as being "probably an undescribed species", but made no mention of Haswell's material. Schmitt (1926) included both Haswell's cotype and McCulloch's Cooktown "*Penaeus mastersii*" with the *Endeavour* "*Penaeopsis monoceros*", and subsequently the estuarine *M. mastersii* was regarded as the deeper-water *M. monoceros*. Burkenroad in Morris and Bennett (1952) was the first to identify *M. mastersii* as a different species. The rostrum and postrostral carina of the cotype figured by Schmitt (1926) could be that of *M. monoceros* but the thelycum is like that of *M. mastersii*. At the time of writing (Dec. 1954) Haswell's cotype could not be located in the Macleay Museum, but was examined by Dr. A. A. Racek about 18 months previously, who states (personal communication) that the specimen was a dried one and immature, but that he did not think it was *M. monoceros*. McCulloch's specimens were identified from Haswell's cotypes and the Australian Museum contains other specimens of *M. mastersii* identified in the same way. While it is quite possible that McCulloch erred in his identification, it seems likely that Haswell's "*Penaeus mastersii*" is the estuarine *Metapenaeus* sp. (Unfortunately Haswell does not state method or depth of collection.) Rather than create a new name for this species, it is preferable to retain Haswell's name, unless well-preserved type material can be located in the Macleay Museum.

The present species is very closely akin to *M. burkenroadi* Kubo. The petasmas of the Western Australian specimens are similar to that figured by de Man (1911, Plate VI, Fig. 15*a*, *b*), and de Man's "*Penaeopsis affinis*" is undoubtedly *M. mastersii*.

The following are the differences between *M. mastersii* (eastern Australia) and *M. burkenroadi* (part latter after Kubo 1949, 1954):

Feature	*M. mastersii*	*M. burkenroadi*
Rostrum ♂	Shorter than antennular peduncle	Longer than antennular peduncle
Abdominal carina on 4th somite	Beginning from anterior	Beginning from middle
Cardiac plate	26–32 spinules	32–35 spinules
Zygocardiac ossicle	7–8/10–12 teeth	10/14 teeth
Median projections of petasma	Retort-shaped, tapering to a more or less blunt point	As wide apically as at base

Feature	*M. mastersii*	*M. burkenroadi*
Posterior thelycum	Lateral edges rounded	Lateral edges almost rectangular

Subspecies of M. mastersii.—There are a number of small but constant differences between specimens from Western Australia (Peel Inlet to Exmouth Gulf) and those from Queensland:

Queensland Specimens	Western Australian Specimens
Posterior ½ of postrostral carina a narrow strip almost to margin of carapace	Carina becoming a wide glabrous strip towards its posterior end
Apical portions of distomedian projections of petasma small (Fig. 18*B*)	Apical portions of distolateral projections of petasma large (Fig. 18*D*)
Anterolateral tubercles of anterior plate of thelycum not much more prominent than the anteromedian tubercle	Anterolateral tubercles of anterior plate of thelycum much more prominent than the barely perceptible anteromedian tubercle
Average length at sexual maturity, ♂ 75 mm, ♀ 95 mm	♂ 65 mm, ♀ 78 mm (Peel Inlet specimens)

This raises the question whether these are valid subspecies. *M. mastersii* appears to become less common in northern Queensland, and there may be a break in its distribution somewhere in northern Australia. The petasma at least appears constant from Indonesia to Perth. Lack of material from northern Australia makes it impossible to decide whether there is a gradual transition here from one set of characters to the other. It may be that this species, being largely estuarine, tends to produce localized races to a greater extent than those spawning in deeper waters, where planktonic larvae would be distributed more widely. The Western Australian specimens are in some respects intermediate between the eastern Australian *M. mastersii* and *M. burkenroadi* Kubo, and future work may show that the 2 species should be united.

Metapenaeus eboracensis, sp. nov.

Fig. 19*A–G*

Material.—Queensland: Mouth Norman River, Gulf of Carpentaria, 1–2 fm, mud, Aug. 1953, coll. T. C. Marshall; holotype ♂, 64 mm, carapace 13·5 mm; allotype ♀, 90 mm, carapace 20·5 mm; paratypes 3 ♂, 45, 46, 48 mm, 5 ♀, 45, 50, 86, 89, 98 mm; Townsville, 20 fm, coll. R. K. Bryson, Aug. 1953, 3 ♂, 52, 62, 62 mm, ♀, 67 mm; Townsville, main beach, 25.vii.1945, 2 ♀, Aust. Mus. regd. No. P11662 (101 mm), P11663 (81 mm); Cairns, mud flats, Aust. Mus. regd. No. P4293, ♀, 43 mm.

Diagnosis

Body with pubescent patches small and widely separated. Rostrum with 6–7 teeth + epigastric, sigmoidal, the distal $\frac{1}{3}$ naked. Adrostral sulcus ending below epigastric tooth. Branchiocardiac carina present reaching $\frac{1}{2}$ carapace. Cardiac plate with 19–20 spinules. Petasma with simple flap-like median projections, appendix masculina with square depression on ventral surface of distal piece. Thelycum with small leaf-shaped anterior plate, posterior plate convex except for median cleft.

Description

Rostrum.—Teeth 6–7 + epigastric; sigmoidal, proximal $\frac{2}{3}$ free portion armed and curving downwards, distal $\frac{1}{3}$ naked and curving upwards; reaching to or slightly exceeding tip of antennular peduncle. Adrostral carina ending between 1st and 2nd teeth, sulcus shallow, feebly defined, and ending below epigastric. Postrostral carina broad and low, posterior $\frac{1}{3}$ indistinct, ending in a glabrous expansion $\frac{1}{10}$ length carapace from its posterior edge. Epigastric and 2nd tooth on carapace, former at $\frac{1}{3}$ carapace.

Carapace.—Gastrofrontal sulcus present, very wide and shallow, bounded posteriorly by postocular sulcus, which lies at angle of 40° to rostrum. Orbito-antennal sulcus shallow and ending in front of hepatic spine. Antennal carina ending $\frac{1}{3}$ distance between antennal and hepatic spine. Cervical sulcus straight, ending at not quite $\frac{1}{2}$ carapace. Hepatic sulcus descending vertically then curving towards pterygostomial angle. Branchiocardiac sulcus present, the anterior end at posterior $\frac{1}{3}$ carapace; carina becoming indistinct at $\frac{1}{2}$ carapace.

Antennules.—Flagella subequal and almost equal to length of peduncle in ♂, equal and $\frac{1}{3}$–$\frac{1}{2}$ length of peduncle in ♀. Prosartema reaching most distal point of junction of ophthalmopod peduncle with cornea. Stylocerite not reaching $\frac{1}{2}$ basal segment.

Antennae.—Flagellum twice length body. Spine of scaphocerite reaching as far as tip of antennular peduncle, exceeded by tip lamellar portion; scaphocerite thrice as long as broad.

Mandible.—Distal segment of palp reaching tip of basicerite, twice as long as wide and twice length basal segment. Incisor process with shallow notch, molar process with smooth raised ventral and anterior edges.

Maxillule.—Basal segment of palp with long spine with base at $\frac{3}{4}$ segment, its tip reaching as far as segment; a row of about 10 long spines on distal $\frac{1}{2}$ posterior face towards the outer edge. Distal segment $\frac{1}{8}$ length basal segment.

Thoracic appendages.—Dactyl of 3rd maxilliped $\frac{3}{4}$ propodus and reaching $\frac{1}{2}$ carpocerite. First pereiopod reaching from tip of basicerite to base of carpocerite; 2nd not quite reaching tip of carpocerite; 3rd reaching from $\frac{1}{2}$ to tip of 2nd antennular segment; 4th barely exceeding tip of basicerite; 5th slender and reaching to or almost to tip of antennular peduncle. Ischium of 1st pereiopod angled but not spinous. Fifth pereiopod ♂ with a very shallow depression and feeble tubercle.

Abdomen.—Dorsally carinated from the anterior of 4th somite. Telson with single row of minute spinules on either side.

Gastric mill (Fig. 19*F*, *G*).—Cardiac plate with 19–20 spinules. Zygocardiac ossicle with upper row of 9–10 tubercles, 1st 2 wide and blunt, and lower row of 8–9 tubercles of which 1st 2 are larger, blunter, and separated from the remainder, which are larger than corresponding tubercles in upper row. Prepyloric ossicle with median rounded tubercle projecting beyond the 9–11 lateral tubercles. Urocardiac ossicle broadly subpentagonal; cardiac ossicle heart-shaped; pterocardiac ossicles together making an angle of about 120° to urocardiac.

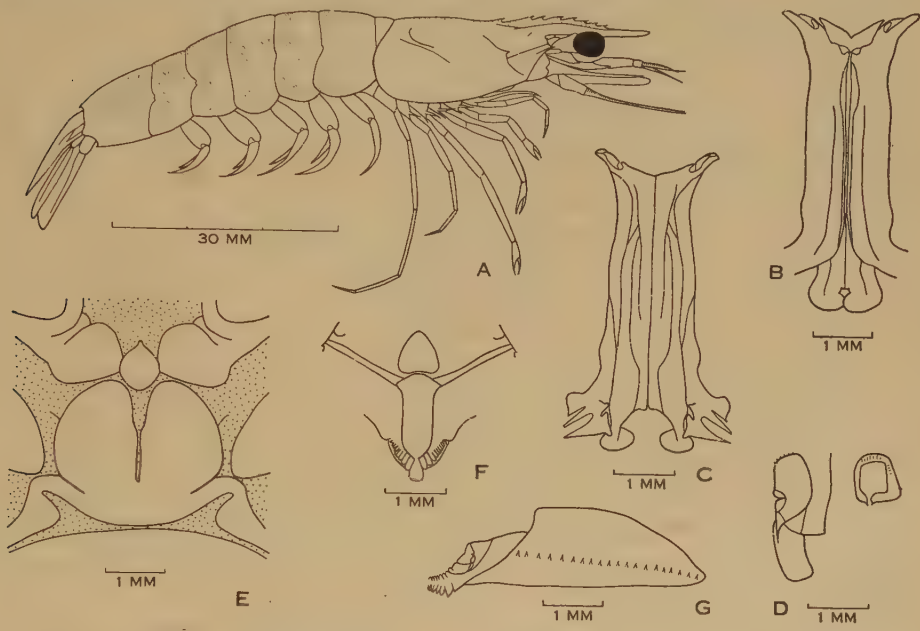

Fig. 19.—*Metapenaeus eboracensis*, sp. nov. *A*, allotype; *B*, ventral surface of petasma of holotype; *C*, dorsal surface of petasma; *D*, appendix masculina and end view of distal piece; *E*, thelycum of allotype; *F*, cardiac, urocardiac, pterocardiac, and prepyloric ossicles; *G*, cardiac plate and zygocardiac ossicle.

Petasma (Fig. 19*B*, *C*).—Median projections flaps closing distal opening of petasma. Distolateral projections slender, attaining ½ coxae of 3rd pereiopods, distance between tips equal ½ total length petasma.

Appendix masculina (Fig. 19*D*).—Distal piece with ovoid dorsal surface; ventral surface with large, more or less square depression of which proximal side runs into a narrow channel; a few small apical setae.

Thelycum (Fig. 19*E*).—Anterior plate small, flat, leaf-shaped, as long as wide, bounded, and level with coxal projections from 4th pereiopods. Posterior plates oval and level with anterior plate; with deep median cleft with rounded edges, otherwise convex. Length posterior plate thrice that of anterior plate. In allotype posterior plate is fused almost completely with sternal plate of 5th pereiopods, but in 81- and 101-mm ♀♀ from Townsville, sternal plate is separated partially from posterior plate by narrow sulcus, latter plate then being completely divided by median cleft and about twice as wide as long.

Colour in life.—Semitransparent, speckled with brown, tips of uropods green. Body with relatively few pubescent patches.

Distribution

So far known only from the vicinity of Cape York, Qld. (hence the specific name), viz. Norman River (Gulf of Carpentaria), Townsville, Cairns.

Discussion

M. eboracensis is similar to *M. dobsoni* (Miers), the petasmas being alike. The thelyca are also similar but as figured by Alcock (1906), the anterior plate of *M. dobsoni* is larger and rounded anteriorly. Further, ♂ *M. eboracensis* has a simple spine on 3rd pereiopod and a feeble meral tubercle on 5th, whereas *M. dobsoni* has a much enlarged barbed basial spine on 3rd pereiopod and 2 tubercles on merus of 5th.

METAPENAEUS MACLEAYI (Haswell)

School Prawn, eastern Australia

Fig. 20*A–F*

Penaeus macleayi Haswell, 1879, p. 40; 1882, p. 210.
Penaeopsis macleayi Schmitt, 1926, pp. 333–8.
Metapeneus macleayi Alcock, 1906, p. 17.
Metapenaeus macleayi Racek, 1955, pp. 228–9.
Penaeus haswelli Phillipps, 1925, p. 3.

Material.—QUEENSLAND: Off Point Lookout, Stradbroke I., 39 specimens, 96–162 mm. NEW SOUTH WALES: Lake Illawarra, 1953, 5 ♀, 118–134 mm. Material has also been examined from Eden Harbour, N.S.W., to Mary River, Qld., and from Australian Museum collection.

Description

Rostrum.—5–6 teeth + epigastric; epigastric absent in large ♂♂, its position indicated by a shallow depression, but present in many immature ♂♂. Tip of rostrum often damaged or malformed but when intact reaching $\frac{1}{2}$ 3rd segment of antennular peduncle in ♂, and as far as tip or exceeding it in ♀. Rostrum sigmoidal, almost $\frac{1}{2}$ free portion naked and usually strongly upcurved. Adrostral carina almost reaching 1st rostral tooth, sulcus shallow, not well defined, reaching beyond epigastric to $\frac{1}{3}$ carapace. Postrostral carina broad and ending at $\frac{2}{3}$ carapace.

Carapace.—Postocular sulcus at angle of 35° to rostrum. Orbito-antennal sulcus wide and deep and meeting hepatic below hepatic spine. Hepatic sulcus descending almost vertically with slight posterior curve for $\frac{3}{7}$ length then turning sharply forward towards pterygostomial angle, lower part but slightly curved; a small isolated horizontal posterior hepatic sulcus $\frac{1}{10}$ length carapace, its anterior end behind hepatic spine. Cervical sulcus deep, slightly curved, and reaching 0·45 length carapace. Branchiocardiac sulcus wide, feeble, $\frac{1}{4}$ length carapace, anterior end at $\frac{1}{3}$ carapace; branchiocardiac carina barely defined below sulcus.

Antennules.—Flagella equal, slightly longer than $\frac{1}{2}$ peduncle in ♂, slightly less than $\frac{1}{2}$ in ♀. Prosartema reaching as far as tip, stylocerite attaining $\frac{1}{2}$ 1st segment.

Thoracic appendages.—Third maxilliped reaching or slightly exceeding tip, 1st pereiopod reaching base of carpocerite; 2nd pereiopod exceeding carpocerite by ½ dactyl; 3rd reaching as far as tip of 2nd segment of antennular peduncle; 4th reaching from base to tip of carpocerite; 5th reaching from base to tip of 2nd segment of antennular peduncle. Ischium of 5th pereiopod in ♂ with keel almost as long as segment, merus with deep notch, followed by a bulbous tubercle slightly reflected outwards.

Abdomen.—Dorsal carina commencing middle 4th somite. Telson with 4 large lateral spines becoming progressively larger towards tip, base of last pair level with end of median sulcus.

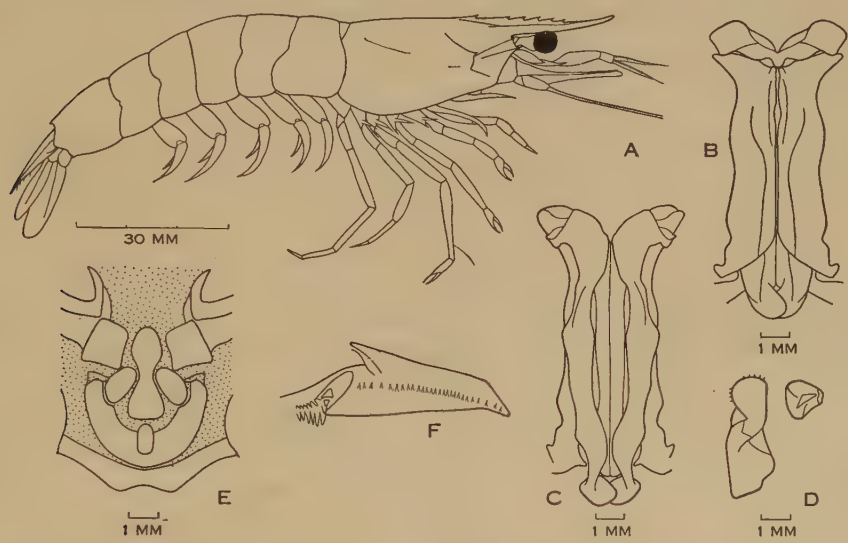

Fig. 20.—*Metapenaeus macleayi* (Haswell). *A*, 129 mm ♀; *B*, ventral surface of petasma, 112 mm ♂; *C*, dorsal surface of petasma; *D*, appendix masculina and end view of distal piece; *E*, thelycum, 132 mm ♀; *F*, cardiac plate and zygocardiac ossicle.

Gastric mill (Fig. 20*F*).—Cardiac plate with 19–28 spinules. Zygocardiac ossicle with upper row of 5–7 short tubercles and lower row of 2 conical tubercles separated from remaining 6–8 long tubercles. Prepyloric ossicle with 7–10 lateral teeth, most lateral 2–4 minute and spinous.

Petasma (Fig. 20*B*, *C*).—Reaching from base to ½ basis of 3rd pereiopods. Mediodistal lobes an inverted cup shape, closing very wide openings of distolateral projections, from which they are separated by shallow indentations in edges of distal openings of petasma. Mediodistal projections extending laterally to exceed distolateral projections, distance between lateral extremities of latter ½ total length petasma.

Appendix masculina (Fig. 20*D*).—Distal piece with rounded apex bearing a number of minute setae, and about equal to length basal piece. Ventral depression an elongate triangular shape.

Thelycum (Fig. 20*E*).—Anterior plate spatulate, the wide part lying anteriorly, concave, and above level of expansions of coxae of 4th pereiopods which bound the narrower part. Coxal expansions produced into a ventral keel. Posterior plates with rounded median process not projecting beyond rest of plate; anterolaterally enclosing 2 prominent ovoid tubercles projecting below level of flat ventral surface of posterior plate. Posterior plate twice as wide as long. Transverse sternite of 5th pereiopods with 2 tufts of long setae.

Appearance in life.—A small pubescent patch at top of cervical sulcus, another 2, very small, anterior to this, and a narrow strip of pubescence above the orbito-antennal sulcus, and on either side of the postrostral carina. Body otherwise glabrous. Body translucent, with olive-green chromatophores; tips of uropods blue. *Estuarine juveniles* (Brisbane River).—Translucent with brown chromatophores, other colours absent.

Distribution

Ranging from Eden Harbour, N.S.W., to Mary River, Qld. One of the common commercial prawns of New South Wales, but not very common in Queensland. Juveniles appear in the Brisbane River in January–March.

Discussion

Burkenroad (1934*a*) states that the description of *M. demani* Roux "seems very like" *M. macleayi*, the former not possessing large spines on telson. However, rostrum, thelycum, and petasma of the 2 species are distinctive, and there is little possibility of confusion. The only other well-established *Metapenaeus* spp. which are mainly glabrous are *M. brevicornis* (Milne Edwards) and *M. spinulatus* Kubo, but these closely related species have distinctive rostra, more or less straight with high blades, and simple hepatic sulci, only the lower portion being present. Thus *M. macleayi* seems to be a quite isolated species both morphologically and geographically.

Genus ATYOPENAEUS (Alcock) (emend.)

Atyopeneus Alcock, 1905, p. 524; 1906, p. 45.
Atyopenaeus de Man, 1911, p. 83. Kubo, 1949, p. 365.

Rostrum dorsally toothed only. Pterygostomial angle blunt; orbito-antennal sulcus and antennal carina absent; no longitudinal sutures on carapace. Antennular flagella longer than carapace; no spine on distoventral border of 1st segment of peduncle. Maxillulary palp with 2 segments. Exopods on all pereiopods; propodus and dactyl of 5th very long and slender. Ischial spines on 1st and 2nd pereiopods, basial spines on 2nd and 3rd. Petasma tubular, lateral lobes forming distolateral openings and with posterior projections. Thelycum with simple open seminal receptacle, anterior plate elongate, posterior plates bar-like. Pleurobranchiae on 2nd–6th thoracic somites; a rudimentary dendroid arthrobranch on 1st thoracic somite; 2nd–6th each with 2 and 7th with a posterior arthrobranch, anterior arthrobranch of this somite represented only by a bar; mastigobranchiae on 1st, 2nd, 4th–6th thoracic somites.

De Man (1911) does not mention presence of a rudimentary arthrobranch on 1st thoracic somite, but Kubo (1949) notes it as being very small in *A. compressipes*

(Henderson). It is also difficult to distinguish in *A. formosus* and it is probable that de Man overlooked it.

The genus comprises 3 species, viz. *A. compressipes* (type species), *A. dearmatus* de Man, and *A. formosus*, sp. nov. *Penaeus stenodactylus* Stimpson possibly belongs to this genus.

Key to the Species of Atyopenaeus

1. Rostrum long, reaching tip of antennular peduncle; petasma with ovoid distolateral projections; thelycum with lanciform anterior plate ..... *A. formosus*, sp. nov.
   Rostrum short, not exceeding 1st segment of antennular peduncle; petasma with more or less acute distolateral projections; thelycum with tongue-like anterior plate 2
2(1). Hepatic spine absent; petasma constricted distally, distolateral projections directed laterally; anterior plate of thelycum pointed anteriorly ..... *A. dearmatus* de Man
   Hepatic spine present; petasma not constricted distally, distolateral projections directed anteriorly; anterior plate of thelycum rounded anteriorly .. *A. compressipes* (Henderson)

Atyopenaeus formosus, sp. nov.

Fig. 21*A–H*

Material.—Queensland: Moreton Bay, off Sandgate, 2–3 fm, sandy mud, 28.xii.1951: holotype ♂, 59 mm, carapace 13 mm; allotype ♀, 80 mm, carapace 20 mm; paratypes, ♂, 56 mm, 6 ♀, 63, 66, 68, 70, 71, 72 mm. Off Cape Moreton, 15.ix.1951, 2 ♂, 27, 55 mm, 3 ♀, 44, 66, 72 mm. 3 miles E. of Redcliffe, Moreton Bay, sandy mud, 3–5 fm, 20.ii.1952, 9 ♀, 66–91 mm; July 1953, 5 ♀, 74–83 mm. Mouth Norman R., Gulf of Carpentaria, 1–2 fm, mud, coll. T. C. Marshall, Aug. 1953, 3 ♀, 51–58 mm.

Diagnosis

Rostrum long, reaching to or beyond tip of antennular peduncle; adrostral and postrostral carinae indistinct. Postorbital sulcus deep, cervical sulcus feeble, short, hepatic sulcus absent. Fourth and 5th abdominal somites with large postero-dorsal spines. Petasma short, wide, with a pair of rounded distolateral projections. Thelycum with lanciform anterior plate, and parallel bar-like posterior plates.

Description

Rostrum.—Teeth 5–8, usually 6, + epigastric. Rostrum long, slender, and upcurved, slightly exceeding tip of antennular peduncle; excepting epigastric, teeth uniformly spaced along its length. A distinct adrostral carina not present, instead a blunt barely defined ridge ending at about 2nd tooth; sulcus absent. Postrostral carina indistinct and not reaching more than $\frac{1}{2}$ carapace, usually less.

Carapace.—Postocular sulcus very deep, indenting base of rostrum, below 2nd rostral tooth, and running at angle of 45° to rostrum; sigmoidal when viewed laterally; a small blunt orbital spine. Antennal and hepatic spines conical; cervical sulcus ill defined, often less than $\frac{1}{10}$ length carapace, its upper limit at 0·35–0·4 length carapace. A wide shallow indentation only in front of and below hepatic spine; no sulcus. Sometimes very feeble indications of a branchiocardiac sulcus.

Eye.—Peduncle slender, cornea (measured anteroposteriorly) about $\frac{1}{7}$ length carapace.

Antennules.—Flagella equal, about twice length antennular peduncle and $1\frac{1}{2}$ length carapace in ♂, nearly twice length antennular peduncle and $1\frac{1}{5}$ length carapace in ♀. Prosartema reaching tip of junction of optic peduncle with cornea. Stylocerite slender, diverging from and projecting above, tip attaining $\frac{2}{3}$ basal segment. Second segment cylindrical, equal length of 1st; 3rd segment $\frac{1}{3}$ length 2nd, often inclined upwards at right angles to it.

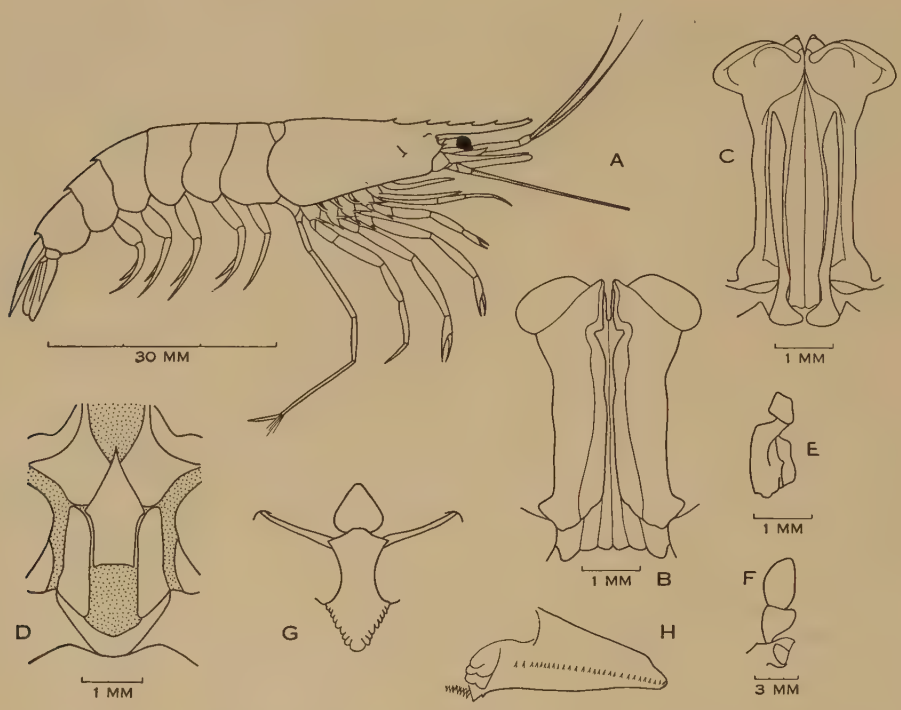

Fig. 21.—*Atyopenaeus formosus*, sp. nov. *A*, allotype; *B*, ventral surface of petasma of holotype; *C*, dorsal surface of petasma; *D*, thelycum of allotype; *E*, appendix masculina; *F*, mandible and palp of allotype; *G*, cardiac, urocardiac, pterocardiac, and prepyloric ossicles of allotype; *H*, cardiac plate and zygocardiac ossicle of allotype.

Antennae.—Length carpocerite $2\frac{1}{2}$ times width, reaching as far as stylocerite. Length scaphocerite 4 times width, reaching $\frac{1}{2}$ 3rd segment of antennular peduncle.

Mandible (Fig. 21*F*).—Palp reaching tip of basicerite, outer edge of distal segment convex, $1\frac{1}{2}$ times length rounded basal segment. Cutting edge of incisor process straight except for a small tooth at anterior extremity; molar process flat except for a low posterior rim rising sharply medially with appearance of a low tubercle.

Maxillule.—Basal segment of palp with angular setose projection on inner basal $\frac{1}{2}$; a large spine on inner edge with base at $\frac{2}{3}$ segment, followed by a smaller spine; posterodistal surface towards outer edge with a spine, with smaller spine on either side. Distal segment narrow, $\frac{1}{4}$ length basal segment.

Thoracic appendages.—Third maxillipeds reaching $\frac{1}{2}$ 2nd segment of antennular peduncle; 1st pereiopod exceeding carpocerite by dactyl; 2nd and 3rd reaching about $\frac{1}{2}$ 2nd segment of antennular peduncle, 4th slightly exceeding its base; 5th reaching as far as or slightly exceeding tip of antennular peduncle. Excepting 5th legs, thoracic appendages with long setae, particularly on ventral edges of 2nd–4th pereiopods. Fifth pereiopods very slender, particularly propodus and carpus, with small tuft of apical setae on propodus.

Abdomen.—Fourth to 6th abdominal somites with high carina, ending on each somite in an acute spine, that of 6th smaller than the others. Abdomen often characteristically flexed between 3rd and 4th somites. Telson unarmed, median sulcus very feeble, only a short proximal depression indicating its position. Telson almost 0·6 length carapace and slightly exceeding uropods. Pleopods long and slender, total length of the 2nd $\frac{4}{5}$ length carapace. Sixth abdominal somite rounded postero-inferiorly, with a very small blunt spine.

Gastric mill (Fig. 21*G*, *H*).—Cardiac plate with 24–30 spinules. Zygocardiac ossicle with 4 large tubercles (2nd and 3rd double) running across cardiac plate, followed at right angles by irregular row of about 20 tubercles which get progressively smaller. Cardiac ossicle cordiform; urocardiac with rounded apex, distolateral sides slightly concave and forming an obtuse angle; pterocardiac ossicles simple, bar-shaped, and making an obtuse angle with urocardiac. Prepyloric with a large median tooth and 7–8 lateral teeth.

Petasma (Fig. 21*B*, *C*).—Reaching $\frac{1}{2}$ bases of 4th pereiopods with prominent ovoid distolateral projections overlying 2 posterodistal plates, together closing distolateral openings of petasma; 2 blunt distomedial projections. Distance between lateral extremities of distolateral projections $\frac{2}{3}$ total length petasma. Median lobes with posterior, blunt incurved projections.

Appendix masculina (Fig. 21*E*).—Distal piece irregularly cuboid and $\frac{1}{3}$ length basal piece.

Thelycum (Fig. 21*D*).—Anterior plate lanciform with oval median depression and spinous apex, coxal projections from 4th pereiopods lying above it; posterior end rectangular, bearing a number of small setae. Two posterior plates a rounded bar shape, enclosing rectangular part of anterior plate; posteriorly these bars meet a pair of V-shaped processes from posterior sternal plate, making a pentagonal seminal receptacle. Coxae of 4th and 5th pereiopods each with tuft of setae.

Appearance in life.—Body and appendages uniformly a striking reddish-pink. Surface of abdomen and carapace minutely and irregularly sculptured.

Distribution

So far known only from the type locality and Norman River, Gulf of Carpentaria. During 1951–1953 it was fairly common in Moreton Bay in catches of *Penaeus plebejus* and *Metapenaeus mastersii*. *Atyopenaeus compressipes* (Henderson) is also common but not abundant in southern Japan, though formerly considered rare (Kubo 1949).

Discussion

Rostrum, thelycum, and petasma of *A. formosus*, in addition to a number of minor features, set this species apart from the remaining members of the genus. All prawns of the genus are small (*A. formosus* apparently being the largest, the females showing gravid ovaries at 60–70 mm), and so far none have been found in the very abundant quantities characteristic of many other Penaeinae.

Genus TRACHYPENAEUS (Alcock) (emend.)

Trachypeneus Alcock, 1901, p. 15; 1906, p. 43. Burkenroad, 1934*b*, pp. 94–6.
Trachypenaeus de Man, 1911, pp. 87–8. Kubo, 1949, pp. 391–2.

Rostrum toothed dorsally only. Carapace with longitudinal sutures which may be very short and barely perceptible; transverse sutures indistinct or absent. Cervical, orbito-antennal, and hepatic sulci often ill defined or absent. Pterygostomial angle sharp or blunt, never spinous. Abdomen usually with pronounced dorsal carination posterior to 3rd somite. Telson with movable lateral spines. First antennular segment without a spine on ventral distomedian border. Antennular flagella much shorter than carapace. Maxillulary palp unsegmented. Petaloid exopods on all pereiopods, 1st and 2nd pereiopods with basial spines. Median lobes of petasma thickened, apices slightly recurved ventrally; lateral lobes bearing large distolateral projections, wide and wing-like extending laterally, or more slender and directed forward. Distal piece of appendix masculina angular, with few to many small distal setae. Thelycum with a broad, thickened anterior plate, often with posterior median pocket-like seminal receptacle as wide as anterior plate. Zygocardiac ossicle with 3 large principal teeth and double row of smaller teeth which get progressively smaller. Pleurobranchiae on 3rd–6th thoracic somites, a rudimentary arthrobranch on 1st, anterior and posterior arthrobranchiae on 2nd–6th, and posterior arthrobranch only on 7th thoracic somites; mastigobranchiae on 1st, 2nd, 6th somites, sometimes also on 4th and 5th. Carapace densely pubescent.

Type species *T. anchoralis* (Bate).

The posterior arthrobranch on 7th thoracic somite is displaced forward in *T. fulvus* and sometimes is actually partially fused at the side with epimeral plate, although actual attachment is on arthroidal membrane, making the arthrobranch deceptively like a pleurobranch in appearance. In *T. curvirostris* (Stimpson) the arthrobranch is also displaced forward, but not quite as much as in *T. fulvus*. This displacement forward may be a feature common to Indo-Pacific *Trachypenaeus* spp.

The small number of closely similar species within the genus makes the division into 2 subgenera (Burkenroad 1934*b*) unnecessary, especially as the subgenera are established largely on the presence or absence of mastigobranchiae on the 1st and 2nd pereiopods.

With the exception of *T. pescadoreensis*, of which ♂ is unknown, species of this genus are well established. *T. pescadoreensis* and *T. granulosus* both have a pair of shallow pockets on either side of the backward projections of the anterior plates of their thelyca, and the petasma of *T. granulosus* has forwardly directed distolateral projections. It is likely that ♂ *T. pescadoreensis* will have a petasma similar to that of *T. granulosus*.

Key to the Species of Trachypenaeus

1. Epipods (mastigobranchiae) on 1st and 2nd pereiopods 2
   Epipods absent from 1st and 2nd pereiopods; (limited to Indo-Pacific) 6
2(1). Ischium 1st leg with a small spine; no spine on basis 3rd maxilliped; carapace with longitudinal suture not reaching beyond hepatic spine 3
   Ischium of 1st leg unarmed; a spine on basis of 3rd maxilliped; carapace with longitudinal suture extending beyond the hepatic spine 4
3(2). Rostrum not extending beyond the eye; telson with 4 pairs of lateral spines (limited to Pacific America) ..... *T. brevisuturae* Burkenroad
   Rostrum exceeding the eye; telson with 3 or 4 pairs of lateral spines (species limited to Indo-Pacific) ..... *T. curvirostris* (Stimpson)
4(2). Telson unarmed (limited to Pacific America) ..... *T. byrdi* Burkenroad
   Telson armed (limited to Atlantic and Pacific America) 5
5(4). Exopod of 5th pereiopod not reaching distal end of basis; telson tapering to point with slight indications of proximal shoulders; colour orange and red ..... *T. similis* (Smith)
   Exopod of 5th pereiopod reaching to or beyond distal end of basis; telson with prominent subapical shoulders; colour lavender and chocolate ..... *T. constrictus* (Stimpson)
6(1). Anterior plate of thelycum with a prominent longitudinal ridge (male unknown) ..... *T. pescadoreensis* Schmitt
   Anterior plate of thelycum flat or concave (not including posterior extensions) 7
7(6). Distolateral projections of petasma directed forwards 8
   Distolateral projections of petasma directed laterally ..... *T. fulvus*, sp. nov.
8(7). Distolateral projections of petasma with spatulate tips, reaching coxae of 3rd pereiopods, posterior plate of thelycum U-shaped, enclosing an open ovoid depression ..... *T. anchoralis* (Bate)
   Distolateral projections of petasma with sharp tips reaching coxae of 4th pereiopods; anterior plate of thelycum with posterior tongue-like extension fused with posterior plate ..... *T. granulosus* (Haswell)

Trachypenaeus curvirostris (Stimpson)

Fig. 22*A–F*

Penaeus curvirostris Stimpson, 1860, p. 44. Kishinouye, 1900, p. 23.
Penaeus granulosus Miers, 1884, p. 295.
Parapenaeus curvirostris Rathbun, 1902, p. 38.
Trachypeneus asper Alcock, 1905, p. 531; 1906, p. 43.
Trachypeneus curvirostris Alcock, 1905, p. 523. Schmitt, 1926, pp. 353–8. Racek, 1955, pp. 235–6.
Trachypenaeus curvirostris Kubo, 1949, pp. 393–5.

Material.—Queensland: Off Point Lookout, 20–30 fm, 4 ♂, 41–72 mm, 6 ♀, 52–87 mm.

Description

Rostrum.—6–9 teeth + epigastric, usually 6–7; reaching tip of 2nd segment of antennular peduncle, strongly upcurved in ♀, sometimes almost straight in ♂, varying in either case with degree of maturity. Adrostral carina faint, reaching to or just beyond 1st tooth; postrostral carina reaching to middle of carapace. Epigastric at $\frac{1}{3}$–$\frac{1}{4}$ length carapace.

Carapace.—Longitudinal suture sometimes barely distinguishable, usually $\frac{1}{5}$–$\frac{1}{7}$ length carapace. Transverse suture extremely faint and irregular. Antennal carina extending half way between antennal and hepatic spines. Hepatic sulcus present,

the spine below or slightly in advance of epigastric. Supra-orbital spine present, pterygostomial angle sharp.

Antennules.—Flagella equal in length, 0·85 length peduncle in mature ♀, 1·1 length peduncle in ♂. Distolateral spine of 1st segment diverging from longitudinal axis and pointing slightly upwards. Prosartema reaching almost as far as eye, stylocerite reaching to $\frac{2}{3}$ basal segment.

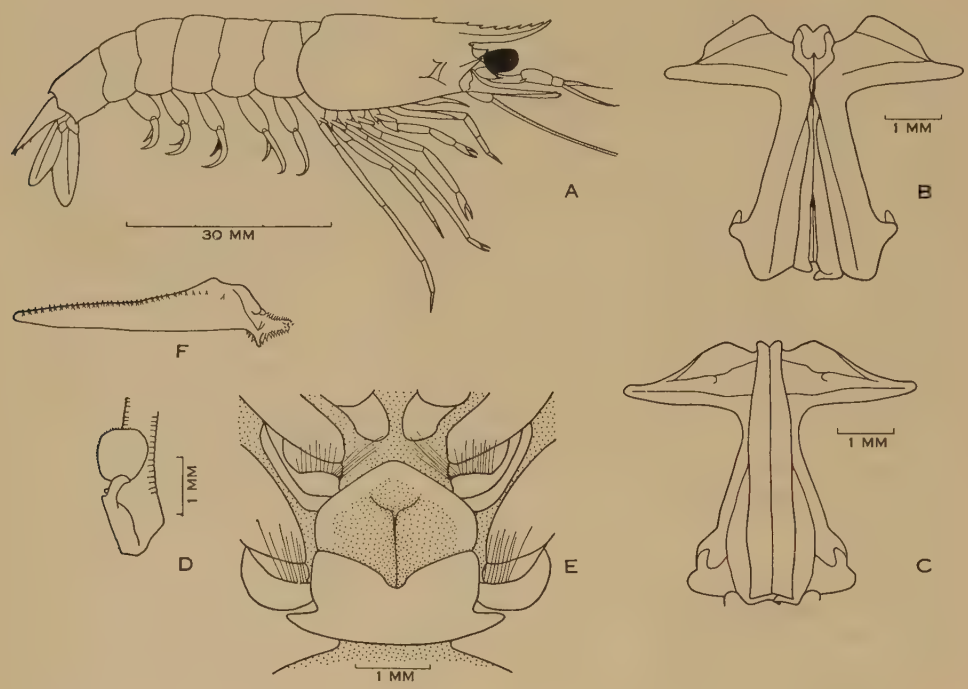

Fig. 22.—*Trachypenaeus curvirostris* (Stimpson). *A*, 84 mm ♀; *B*, ventral surface of petasma, 60 mm ♂; *C*, dorsal surface of petasma; *D*, appendix masculina; *E*, thelycum, 51 mm ♀; *F*, cardiac plate and zygocardiac ossicle.

Antennae.—Scale reaching as far as or slightly exceeding tip of antennular peduncle.

Thoracic appendages.—Endopod of 3rd maxilliped exceeding tip of basal segment of antennular peduncle by $\frac{1}{2}$ dactyl. First pereiopod reaching to or slightly exceeding base of carpocerite, 2nd exceeding it by dactyl; 3rd reaching to or almost to tip of antennular peduncle; 4th reaching as far as stylocerite; 5th reaching from base to tip of 2nd segment of antennular peduncle. Epipodites on 1st 3 pereiopods, a small ischial spine on 1st.

Abdomen.—A small median dorsal tubercle on 2nd, dorsal carina proper beginning at anterior $\frac{1}{3}$–$\frac{1}{4}$ of 4th somite. Telson with 3 pairs of easily discernible spines, the subapical but slightly larger than remaining 2 pairs, and borne on very slight projections.

Gastric mill (Fig. 22*F*).—Cardiac plate with 29–35 spinules; zygocardiac ossicle, 3 principal + 2 longitudinal rows each of 8–12 smaller teeth; prepyloric with 10–12 rounded lateral teeth.

Petasma (Fig. 22*B*, *C*).—Width lateral projections 1·0–1·1 times length petasma. Anterior projections from median plates overhanging apical opening by $\frac{3}{4}$ its diameter.

Appendix masculina (Fig. 22*D*).—Distal piece globular, as wide as long, $\frac{1}{2}$ length basal piece, inner and distal edges fringed with minute setae.

Thelycum (Fig. 22*E*).—Anterior plate with bluntly pointed anterior margin and with median shallow groove which widens out in anterior $\frac{1}{2}$ to form concave depression. Anterior edges of seminal receptacle meeting at obtuse angle with median notch, giving anterior plate a rhombic outline. Spermatophore mass hard and very firmly cemented in receptacle. Coxae of 4th legs with plate-like projection densely fringed with setae, and tuft of setae on coxae of 5th legs. Sternal plate of 5th pereiopods tomentose.

Colour.—Body pink to reddish brown, pereiopods whitish.

Distribution

Off Point Lookout, and off Fraser I., Qld. Japan, Hakodate to Kagoshima and Nagasaki, to depth of 150 m, and Inland Sea; Formosa; Indonesia; Halmaheira Sea; off Selawatti I., south of Timor, Molo Strait, 18–141 fm; Australia, Port Darwin, Thursday I. (Schmitt 1926). Generally found in deeper waters (20–30 fm) than *T. fulvus*, which is common in waters of 2–3 fm.

Discussion

T. curvirostris may readily be distinguished from *T. fulvus* by the following features:

Feature	*T. curvirostris*	*T. fulvus*
Epipodites 1st and 2nd pereiopods	Present	Absent
Hepatic sulcus	Present	Absent
Fifth pereiopod	Not extending beyond 2nd segment of antennular peduncle	Reaching at least to tip of peduncle
Cardiac plate	29–35 spinules	22–28 spinules
Zygocardiac ossicle	2 rows 8–12 small teeth	1 row 7–11, 1 row 15–30 teeth
Thelycum	Anterior plate rhombic; 4th pereiopod with coxal plate	Anterior plate semicircular; no coxal plate on 4th pereiopod
Telson	3 pairs distinct spines, subapical pair not on prominent shoulders	A pair of large subapical spines on prominent shoulders, and 2 pairs of minute spines

The petasma has no marked distinguishing features from that of *T. fulvus*, but the incurved posterior projections of median lobes are much shorter and blunter than those of *T. fulvus*.

Kubo (1949) has shown that the rostrum varies greatly with age, and to a lesser extent with sex, being straighter in smaller specimens and males, and becoming more strongly upcurved in females. Thus degree of curvature of the rostrum is a poor specific feature. The above specimens are at variance with those described by Kubo (1949) in the following features:

Feature	Present Description	Kubo (1949)
Length antennular flagella	♂ 1·1, ♀ 0·85 length peduncle	♂ 0·6–0·7, ♀ 0·45–0·6 length peduncle
Prepyloric ossicle	10–12 lateral teeth	About 23 teeth, 10 of which are minute

Schmitt (1926) observes that length of antennular flagella varies greatly, and lack of minute teeth of prepyloric ossicles does not warrant a separation from *T. curvirostris*. A further difference between the present specimens and those of de Man (1911) and Schmitt (1926), is that there are but 3 pairs of spines on the telsons, whereas both authors refer to 4 pairs. Nor is there any trace of a pit for a minute tooth between subapical and next pair of distinct spines as noted by Schmitt. It seems reasonable to assume that there is specific variation in this respect.

Trachypenaeus fulvus, sp. nov.

Fig. 23*A–G*

Material.—QUEENSLAND: Townsville, Aug. 1953: holotype ♂, 51 mm; allotype ♀, 64 mm; paratypes, 3 ♂, 47, 49, 49 mm, ♀, 64 mm. Moreton Bay, 28.xii.1951, paratypes, 4 ♂, 49–55 mm, 12 ♀, 46–103 mm. Moreton Bay, 17.viii.1951, 2 ♂, 51, 63 mm, 4 ♀, 32–55 mm. Brisbane R., Hamilton, 14.i.1954, 24 postlarvae, 10–25 mm. Norman R., Gulf of Carpentaria, Aug. 1953, 2 ♀, 62, 68 mm. WESTERN AUSTRALIA: Hampton Harbour, 5.ix.1952, 3 ♂, 47–60 mm. Numerous specimens from Exmouth Gulf.

Diagnosis

Rostrum more or less straight, usually with 7–8 teeth + epigastric. Third and 5th pereiopods reaching to or beyond tip of antennular peduncle. Telson with 2 subapical and 4 minute lateral spines. Anterior plate of thelycum semicircular, sternal plate of 5th pereiopods glabrous, no setae on coxae of 4th pereiopods.

Description

Rostrum.—Teeth 6–9 + epigastric (usually about equal numbers with 7 or with 8 teeth + epigastric). Rostrum reaching to or almost to tip of 2nd segment of antennular peduncle, dorsal surface usually straight, ventral surface convex, giving tip a slightly upcurved appearance. Adrostral carina reaching 1st tooth, postrostral carina reaching posterior border of carapace. Epigastric at $\frac{1}{4}$ length carapace.

Carapace.—Sulci and carinae feeble; longitudinal suture sometimes indistinct, $\frac{1}{6}$–$\frac{1}{7}$ length carapace; a small transverse suture present. Antennal carina reaching $\frac{1}{2}$ distance between antennal and hepatic spines. Cervical sulcus not defined, sometimes a faint indication thereof at hepatic spine, latter usually conical and slightly in advance of epigastric. Supra-orbital spine present, pterygostomial angle blunt.

Antennules.—Flagella equal in length, equal to length peduncle. Distolateral spine of basal segment diverging at an angle from longitudinal but in plane of horizontal axis. Prosartema barely exceeding tip of junction of peduncle of eye with cornea. Stylocerite $\frac{1}{2}$ basal segment.

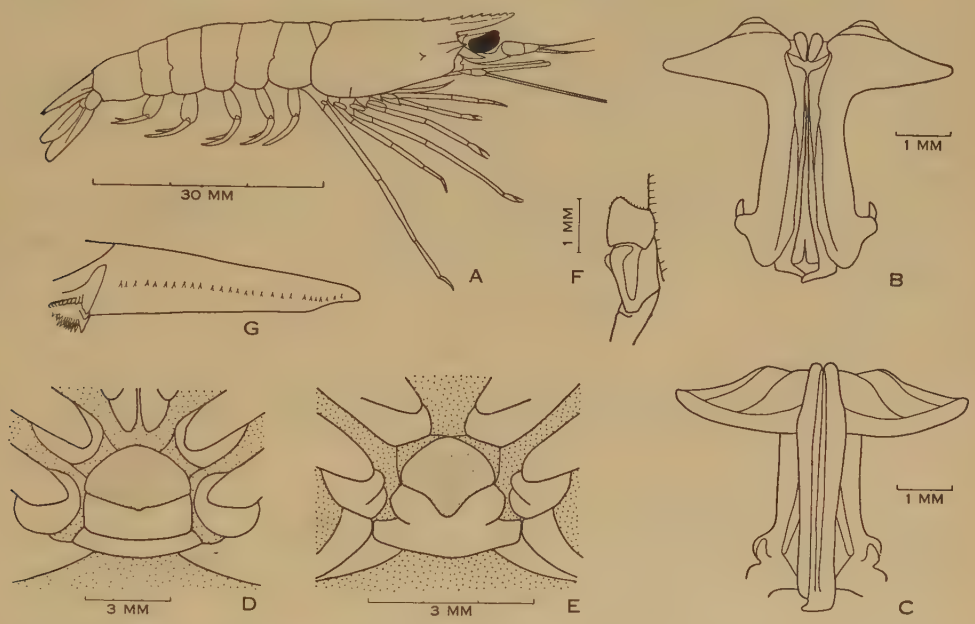

Fig. 23.—*Trachypenaeus fulvus*, sp. nov. *A*, 64 mm allotype, Townsville; *B*, ventral surface of petasma, 52 mm holotype; *C*, dorsal surface of petasma; *D*, thelycum, 86 mm ♀, Moreton Bay; *E*, 52 mm ♀, Moreton Bay; *F*, appendix masculina; *G*, cardiac plate and zygocardiac ossicle.

Antennae.—Scale extending beyond tip of antennular peduncle.

Mandibular palp.—Distal segment reaching tip basicerite length twice its greatest width.

Thoracic appendages.—Endopod of 3rd maxilliped reaching to or slightly beyond tip of basal segment of antennular peduncle; 1st pereiopod reaching tip of or slightly exceeding carpocerite; 2nd from base to tip of 2nd segment of antennular peduncle, 3rd from tip of peduncle to exceeding it by chela; 4th exceeding carpocerite by dactyl; 5th reaching to or beyond antennular peduncle, but usually reaching to base of dactyl of 3rd. An epipod on 3rd pereiopod only. A small ischial spine on 1st pereiopod.

Abdomen.—An elongate median dorsal tubercle on 2nd, dorsal carina proper beginning at anterior $\frac{1}{3}$ of 4th somite. Telson with a pair of large subapical spines

arising from marked projections, with 2 pairs of minute lateral spines; occasionally with some of these spines missing. Length of telson thrice width at base.

Gastric mill (Fig. 23*G*).—Cardiac plate with 22–28 spinules, usually 26–28, zygocardiac ossicle 3 principal teeth + an upper single row of 7–11 teeth and a lower double row of 15–30 teeth. Urocardiac ossicle trapezoidal, prepyloric with concave sides bearing 11–15 rounded teeth.

Petasma (Fig. 23*B*, *C*).—Width lateral projections 1·1–1·2 times length petasma. Median plates with anterior projections overhanging the opening by $\frac{3}{4}$ its diameter.

Appendix masculina (Fig. 23*F*).—Distal piece hemicylindrical, width equal to length, inner edge slightly longer than outer, distal edge slightly concave and fringed with a few small setae. Anterior piece $\frac{3}{4}$ length basal piece.

Thelycum (Fig. 23*D*, *E*).—Anterior plate with semicircular front edge. Anterior edge of seminal receptacle deeply notched in small unimpregnated females, notch tending to be much reduced or obliterated in impregnated females, the anterior edge becoming shallowly concave. Sternal plate of 5th pereiopods smooth.

Colour in life.—Body densely pubescent, varying from mid to light yellowish brown; pleopods usually light-brown, pereiopods darker, eyes with a distinct green iridescence.

Distribution

Moreton Bay to Norman River, Gulf of Carpentaria; north-western Australia. Sometimes quite common, approaching commercial abundance in Moreton Bay, in catches of *Penaeus plebejus* and *Metapenaeus mastersii*.

Discussion

Although Schmitt (1926) gives reasons for regarding *T. asper* Alcock, 1906, as a synonym of *T. curvirostris*, Kubo (1949) regards a Japanese species as *T. asper*. There seems little doubt that *T. asper* as described by Alcock was *T. curvirostris*, a further point in support of this being that the colour of *T. asper* and *T. curvirostris* is the same. This raises the point whether the specimens described by Kubo are *T. fulvus* or another new species. The following are the principal differences between *T. fulvus* and "*T. asper*":

Feature	*T. fulvus*	"*T. asper*" (Kubo's description)
First pereiopod	Barely exceeding carpocerite	Reaching tip of basal segment of antennular peduncle
Second pereiopod	Not exceeding 2nd segment of antennular peduncle	Reaching tip of peduncle
Third pereiopod	Not exceeding tip of antennular peduncle by more than chela	Exceeding tip of peduncle by part of carpus

Feature	*T. fulvus*	"*T. asper*" (Kubo's description)
Fourth pereiopod	Exceeding carpocerite by dactyl	Reaching tip of 2nd segment of antennular peduncle
Fifth pereiopod	Rarely exceeding antennular peduncle by more than dactyl	Exceeding peduncle by ½ propodus
Telson	3 pairs lateral spinules, 2 of which are minute	2 pairs of lateral spinules
Cardiac plate	22–28 spinules	35–39 spinules

Although lengths of pereiopods are variable within *T. fulvus* the range for Australian specimens does not cover lengths given by Kubo (1949) for "*T. asper*". Thelycum, petasma, and appendix masculina appear to be indistinguishable and may be evidence for regarding Kubo's "*T. asper*" as *T. fulvus*. Nevertheless, until specimens intermediate with regard to the above features are found, it seems best to regard Kubo's specimens as doubtful.

Trachypenaeus anchoralis (Bate)

Fig. 24*A–G*

Penaeus anchoralis Bate, 1888, p. 258, pl. XXXV, fig. 1 (female only).
Trachypeneus anchoralis Schmitt, 1926, pp. 348–51. Racek, 1955, pp. 236–7.

Material.—Western Australia: Exmouth Gulf, 24.ix.1954, coll. K. Godfrey, 2 ♂, 53 mm, 36 ♀, 55–77 mm. Queensland: Bowen (Aust. Mus. regd. No. P3528), ♂, 47 mm.

Description

Rostrum.—Teeth 8–9 + epigastric; reaching tip of 2nd segment of antennular peduncle, slightly upcurved in ♂, strongly upcurved in ♀. Epigastric at ¼ carapace. Adrostral carina reaching just behind 1st rostral tooth. Postrostral carina well defined, reaching posterior border of carapace.

Carapace.—Transverse sutures absent, longitudinal sutures barely perceptible, and ⅓ length carapace. Antennal carina extending to ⅓ distance between antennal and hepatic spines. Supra-orbital spine and shallow postocular sulcus present. Cervical sulcus shallow, reaching ½ carapace, length ¼ carapace. Hepatic sulcus wide and deep immediately below and posterior to hepatic spine, becoming narrow and shallow in front of spine, ending in wide depression immediately behind sharp pterygostomial angle. Antennal carina reaching ½ distance between antennal and hepatic spines. Sulci partly obscured by dense pubescence.

Antennules.—Flagella equal in length, 0·9–1·0 peduncle in ♂, and 0·8 length peduncle in ♀. Distolateral spine on basal joint diverging laterally from longitudinal

axis of peduncle. Prosartema reaching as far as tip of eye. Stylocerite reaching $\frac{1}{2}$ basal segment.

Antennae.—Scaphocerite reaching as far as tip of antennular peduncle.

Thoracic appendages.—Third maxillipeds reaching as far as basal segment of antennular peduncle, dactyl slender and propodus with longitudinal row of spinules on distomedian edge; 1st pereiopod reaching $\frac{1}{2}$ carpocerite, 2nd exceeding it by dactyl; 3rd reaching tip of antennular peduncle; 4th reaching as far as or slightly exceeding tip of carpocerite; 5th slender, reaching base of dactyl of 3rd pereiopod. Ischial spine on 1st pereiopod. A lamellar mastigobranch on 3rd pereiopod only.

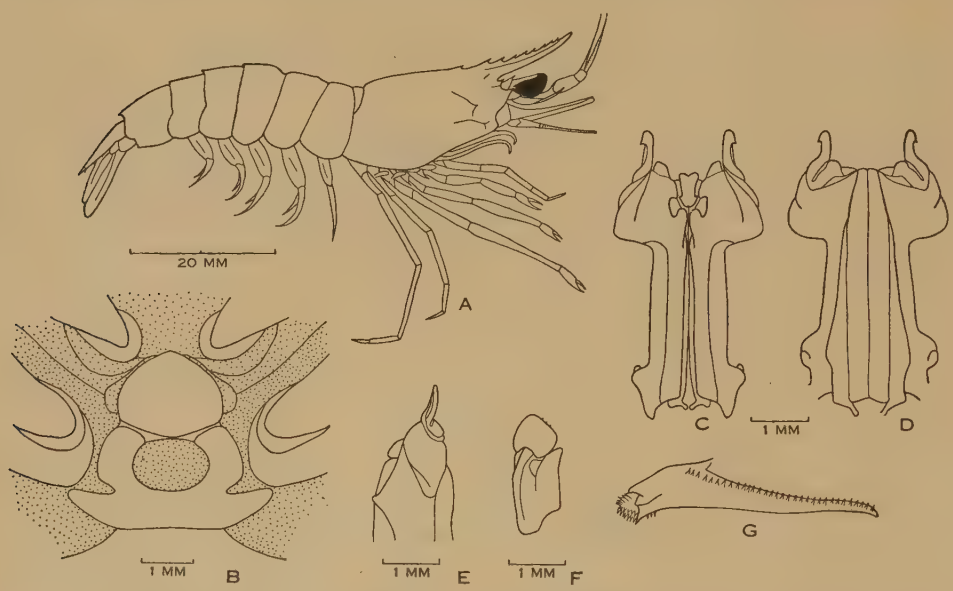

Fig. 24.—*Trachypenaeus anchoralis* (Bate). *A*, 74 mm ♀, Exmouth Gulf; *B*, thelycum, 74 mm ♀; *C*, ventral surface of petasma, 53 mm ♂; *D*, dorsal surface of petasma, 53 mm ♂; *E*, lateral aspect of distal half of petasma; *F*, appendix masculina, 53 mm ♂; *G*, cardiac plate and zygocardiac ossicle, 74 mm ♀.

Abdomen.—Second somite with elongate dorsal tubercle, 3rd with the posterior $\frac{2}{3}$ dorsally carinated, 4th–6th strongly carinated. Telson with 3 pairs of lateral spines, subapical small and borne on small shoulders, the remaining 2 minute and barely perceptible.

Gastric mill (Fig. 24*G*).—Cardiac plate with 26–32 spinules. Zygocardiac ossicle principal teeth + an upper row of 8–10 of which the 1st 2 are blunt, and lower double row of 12–16 teeth meeting upper row; 3–4 small teeth on lower edge of cardiac plate; prepyloric with 12–15 lateral teeth.

Petasma (Fig. 24*C–E*).—Distolateral projections of lateral lobes twisted anteriorly, the extremities more or less parallel, spatulate with a distolateral recurved spinous projection, and reaching coxae of 3rd pereiopods.

Appendix masculina (Fig. 24*F*).—Distal piece bluntly conical, apex inclined medially, with a few minute distolateral spinules; length equal to width and 0·6 length basal piece.

Thelycum (Fig. 24*B*).—Anterior plate slightly concave, closely bounded on its anterolateral edges by coxae of 4th pereiopods. Seminal receptacle a simple, completely open, suboval depression; bounded posteriorly by transverse sternal plate of 5th pereiopods, laterally by flat curved forward extensions of sternal plate, and anteriorly by edge of anterior plate. Spermatophore closely and firmly cemented in seminal receptacle.

Discussion

Superficially this species resembles *T. curvirostris*, but apart from the distinctive petasma and thelycum, does not possess mastigobranchiae on 1st and 2nd pereiopods.

Trachypenaeus granulosus (Haswell)

Fig. 25*A–F*

Penaeus granulosus Haswell, 1879, p. 41; 1882, p. 202 (♀ only).
Trachypeneus granulosus Schmitt, 1926, pp. 351–3.
Trachypenaeus salaco de Man, 1907, p. 135; 1911, pp. 90–2.

Material (part examined by Schmitt (1926)).—Queensland: Bowen (Aust. Mus. regd. Nos. E3116, P3527, E6727, P3529), 4 ♀, 80–84 mm; Darnley I., Torres Strait (Macleay Mus. coll.), ♀, 80 mm (possibly holotype but not marked), 3 ♀, 45–72 mm; Albany Passage, Cape York, coll. M. Ward, ♂, 43 mm.

Description

Rostrum.—Teeth 8–9 + epigastric; reaching to or almost to tip of 2nd segment of antennular peduncle, dorsal surface straight or slightly upcurved at tip, ventral surface convex, accentuating upcurved appearance of tip of rostrum. Adrostral carina reaching 1st tooth, postrostral carina distinct, reaching posterior border of carapace. Epigastric at $\frac{1}{4}$ length carapace.

Carapace.—Longitudinal and transverse sutures distinct, former very short, $\frac{1}{9}$ length carapace. Antennal carina reaching $\frac{1}{3}$ distance between antennal and hepatic spines. Cervical and hepatic sulci sometimes obscured by dense pubescence, removal revealing short distinct cervical sulcus reaching $\frac{1}{2}$ carapace and hepatic sulcus, beginning behind hepatic spine, descending to deep depression below it; sometimes continuing distinctly almost to pterygostomial angle. Hepatic spine slightly in advance of epigastric. Supra-orbital spine small; pterygostomial angle quadrangular.

Antennules.—Flagella equal to length peduncle. Distolateral spine of 1st segment diverging from longitudinal, but in plane of horizontal axis. Prosartema reaching almost as far as tip of eye. Stylocerite reaching $\frac{1}{2}$–$\frac{2}{3}$ length basal segment.

Antennae.—Scaphocerite reaching as far as tip of antennular peduncle.

Thoracic appendages.—Third maxilliped variable in length, reaching from $\frac{1}{2}$ 2nd to tip of 3rd segment of antennular peduncle; 1st pereiopod reaching tip of or exceeding carpocerite by dactyl; 2nd reaching from $\frac{1}{2}$ to tip of 2nd segment of antennular peduncle; 3rd exceeding the peduncle by at least chela; 4th exceeding

carpocerite by dactyl; 5th exceeding antennular peduncle by $\frac{1}{3}$ propodus. An epipodite on 3rd pereiopod only. A small ischial spine on 1st pereiopod.

Abdomen.—An elongate median dorsal tubercle at anterior $\frac{1}{3}$ of 2nd somite, dorsal carina proper beginning anterior $\frac{1}{3}$ of 4th somite. Telson with pair of large subapical spines arising from appreciable projections, with 2 pairs minute lateral spines. Pleuron 1st somite with small ventral notch.

Gastric mill (Fig. 25*F*).—Cardiac plate with 31–35 spinules. Zygocardiac ossicle with principal + an upper row of up to 12 teeth and lower row ending in cluster of minute teeth; several small spines on lower edge of cardiac plate; prepyloric with concave sides each with 12–15 teeth.

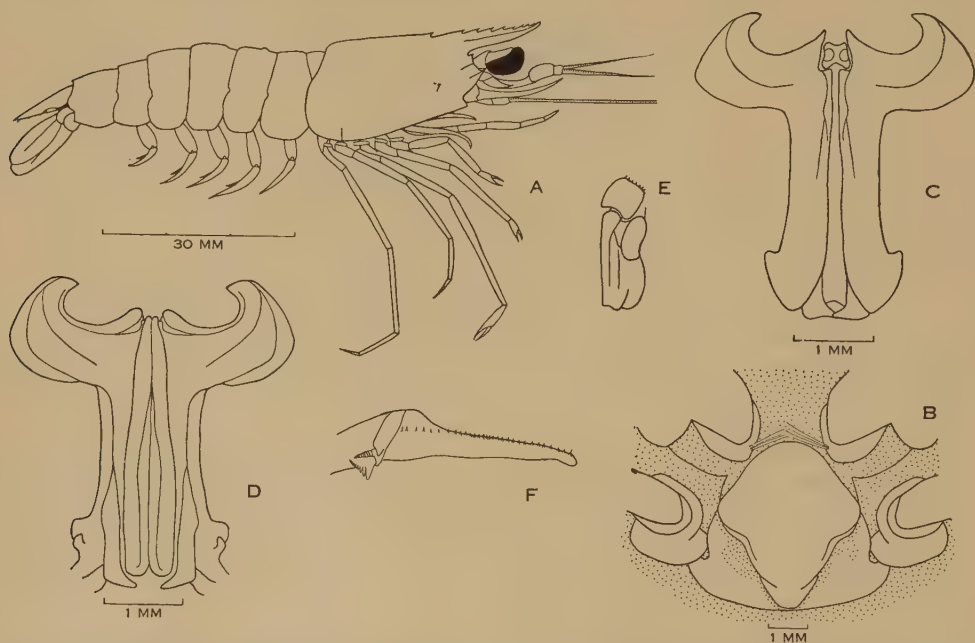

Fig. 25.—*Trachypenaeus granulosus* (Haswell). *A*, 84 mm ♀; *B*, thelycum of same; *C*, ventral surface of petasma, 43 mm ♂; *D*, dorsal surface of petasma; *E*, appendix masculina; *F*, cardiac plate and zygocardiac ossicle.

Petasma (Fig. 25*C*, *D*).—Reaching bases of 3rd pereiopods, greatest width across distolateral projections almost equal to length petasma. Distolateral projections broad, tips curving forward in a broad sweep and ending in inwardly directed mucronate tips; anterior edges reflected dorsally and forming blunt median projections. Median lobes ending in projections completely closing distal opening of petasma.

Appendix masculina (Fig. 25*E*).—Distal piece subrectangular in outline and with a distal fringe of minute setae, and $\frac{1}{2}$ length proximal piece.

Thelycum (Fig. 25*B*).—Anterior plate rounded, the anterolateral margins very slightly concave. Ventral surface of plate concave, with posterior rounded convex projection fused with posterior plate, and extending to posterior margin of latter. Posterior plate excavate on either side of median convexity, the depressions

extending as shallow pockets under indented posterolateral margin of anterior plate. Coxae of 4th pereiopods each with small tuft of inwardly directed setae. Anterior and posterior plate of thelycum covered with minute scattered tubercles.

Distribution

7 and 12 miles NNE. Bowen (Schmitt 1926); Darnley I., Torres Strait (type locality (Haswell 1879)); Albany Passage, Cape York; Lohio Bay, Buton Strait, Kei Is. (de Man 1911). This species must at present be considered rare.

Discussion

Apart from secondary sexual characters this species has few features enabling it to be readily distinguished from *T. fulvus*, carapace and rostrum in particular being almost identical. Apart from the distinctive secondary sexual characters the following are the principal distinguishing features:

Feature	*T. granulosus*	*T. fulvus*
Pterygostomial angle	Quadrangular	Not angular
Antennal scale	Reaching tip of antennular peduncle	Exceeding antennular peduncle
Fourth pereiopod	Exceeding carpocerite by dactyl	Exceeding basicerite by dactyl
Cardiac plate	28–35 spinules	22–28 spinules

Both de Man (1911) and Schmitt (1926) raise the possibility of *T. salaco* de Man being synonymous with *T. granulosus*. The 43 mm male agrees in all external features with the females of *T. granulosus*, and the correspondence of armature of the respective gastric mills removes all doubt of the identity of *T. salaco*. The petasma of the male is undoubtedly the same as that figured by de Man for the latter species.

Genus PARAPENAEOPSIS (Alcock) (emend.)

Parapeneopsis Alcock, 1901, p. 14; 1906, pp. 34–5.

Parapenaeopsis de Man, 1911, pp. 92–3. Burkenroad, 1934*a*, pp. 58–9. Kubo, 1949, pp. 368–70. Barnard, 1950, p. 604.

Rostrum dorsally toothed only. Carapace with longitudinal sutures not reaching as far as median posterior border of carapace and with transverse sutures at base of 3rd or 4th pereiopods. Cervical and orbito-antennal sulci rather feeble; hepatic sulcus present, usually well developed anteriorly. Antennal and hepatic carinae often present. Pterygostomial angle without a spine. Telson armed with small spinules or unarmed. First segment of antennular peduncle without a spine on ventral distomedian border. Maxillulary palp usually with 2 segments, sometimes unsegmented. Exopods on all pereiopods. Petasma tubular, median lobes with simple apices or produced into laterally directed processes; lateral lobes with short

simple spout-like or long, more or less complex distolateral projections, and with proximolateral projections which may be very large. Appendix masculina with 2 or 3 segments, the proximal large in relation to distal segments. Thelycum with a broad, usually concave anterior plate, the posterior plate usually slightly broader than the anterior. Zygocardiac ossicle consisting of 3 large teeth and 2 irregular rows of much smaller teeth. Pleurobranchiae on 3rd–6th thoracic somites; a rudimentary arthrobranch on 1st, anterior and posterior arthrobranchiae on 2nd–6th, and posterior arthrobranch on 7th thoracic somites; mastigobranchiae on 1st, 2nd, sometimes on 4th and 5th thoracic somites. Carapace often minutely pitted.

Type species *P. stylifera* (Milne Edwards).

The genus comprises 14 species, of which *P. atlantica* Balss is found in the Atlantic.

The gender of *Parapenaeopsis* according to the rules of grammar is feminine, but as most authors have treated it as masculine gender, and as there is a possibility of the gender being decided by the International Commission of Zoological Nomenclature (Dr. L. B. Holthuis, personal communication), the gender of specific names has been left unaltered.

Key to the Indo-Pacific Species of Parapenaeopsis

1. Mastigobranchiae on 1st and 2nd pereiopods 2
   Mastigobranchiae absent on 1st and 2nd pereiopods 10

2(1). First pereiopods with basial spines 3
   First pereiopods without basial spines 9

3(2). Second pereiopods with basial spines 4
   Second pereiopods without basial spines ..... *P. uncta* (Alcock)

4(3). Telson with pair of fixed subapical spines; at least distal ½ free portion of rostrum unarmed ..... *P. stylifera* (Milne Edwards)
   Telson without fixed subapical spines, with or without lateral movable spines; ⅓ or less free portion of rostrum unarmed 5

5(4). Petasma with pair of long slender caliper-like distolateral projections directed forwards; thelycum with median tuft of long setae behind posterior edge of last thoracic sternite 6
   Petasma with a pair of distolateral projections directed laterally or distolaterally, usually short and spout-like 7

6(5). Third pereiopods ♀ with basial spine; cardiac plate with 56–59 spinules ..... *P. maxillipedo* (Alcock)
   Third pereiopods ♀ without basial spine; cardiac plate with 42–49 spinules ..... *P. cornutus* (Kishinouye)

7(5). Postrostral carina reaching almost to posterior border of carapace; petasma with pair of short spout-like distolateral projections, and pair of cap-like distal projections 8
   Postrostral carina reaching ¾ carapace; petasma with pair of distolateral projections directed laterally, cap-like distal projections absent ..... *P. nana* (Alcock)

8(7). Antennular flagella 0·5–0·6 length of carapace; thelycum with median tuft of setae on posterior plate ..... *P. sculptilis* (Heller)
   Antennular flagella 0·7 length carapace or longer; thelycum without a median tuft of setae on posterior plate ..... *P. hardwickii* (Miers)

9(2). Epigastric tooth present (species restricted to Pacific America) ..... *P. balli* Burkenroad
   Epigastric tooth absent (species found other than in Pacific America) ..... *P. gracillima* Nobili

10(1). Epigastric tooth present 11
   Epigastric tooth absent 12

11(10). Rostrum exceeding tip of antennular peduncle; longitudinal suture extending to about 0·9 length carapace from anterior edge ..... *P. hungerfordi* (Alcock)
Rostrum short, reaching tip of 1st segment of antennular peduncle; longitudinal suture reaching as far as hepatic spine ..... *P. venusta* de Man

12(10). Anterior plate of thelycum with V-shaped posterior edge, and 2 accessory ridges on anterior edge of posterior plate; rostrum with proximal $\frac{1}{3}$ rising from carapace, remainder more or less horizontal ..... *P. tenellus* (Bate)
Anterior plate of thelycum with a more or less straight transverse posterior edge, no accessory ridges on anterior edge of posterior plate; rostrum inclined upwards at an angle to carapace for whole of its length ..... *P. acclivirostris* (Alcock)

Parapenaeopsis cornutus (Kishinouye)

Fig. 26*A–F*

Penaeus cornutus Kishinouye, 1900, p. 23, pl. 7, fig. 9.
Penaeus sp. Osada, Tanizaki, and Nakazawa, 1931, pp. 6–7.
Parapenaeopsis cornuta de Man, 1911, p. 93.
Parapenaeopsis cornutus Maki and Tsuchiya, 1923, pp. 43–4. Kubo, 1949, pp. 374–8.

Material.—Queensland: Townsville, 20 fm, Aug. 1953, ♂, 73 mm, 3 ♀, 67, 81, 82 mm; Townsville, main beach, 25.viii.1945 (Aust. Mus. regd. No. P11659), ♀, 82 mm.

Description

Rostrum.—Teeth 6–7 + epigastric; sigmoidal, distal $\frac{1}{3}$ unarmed, strongly upcurved and reaching to 3rd segment of antennular peduncle. Adrostral carina ending half way between 1st and 2nd rostral teeth, sulcus shallow. Postrostral carina widening and becoming indistinct posteriorly, ending $\frac{1}{10}$ length carapace from posterior edge; with a small, very feeble sulcus at $\frac{1}{2}$ its length, sulcus $\frac{1}{10}$ length carapace. Epigastric and 1st tooth on carapace, former at $\frac{1}{4}$ carapace.

Carapace.—Orbital spine and postocular sulcus present, latter shallow and at angle 45° to rostrum. Longitudinal suture sometimes indistinct posteriorly, but usually reaching $\frac{1}{2}$ carapace. Cervical sulcus sometimes very indistinct, and meeting longitudinal suture. Antennal carina ending below hepatic spine. Posterior hepatic sulcus and carina of equal length, sinuous and running from behind hepatic spine towards pterygostomial angle, sulcus then turning sharply and continuing towards antennal spine, making a V-shape. A shallow branchiocardiac sulcus $\frac{1}{4}$ length carapace, its anterior end $\frac{2}{3}$ length carapace from orbital spine.

Antennules.—Flagella equal in length, the outer thicker, 0·7 length carapace and $\frac{1}{2}$ length peduncle in ♂, 0·6 length carapace and $\frac{2}{5}$ length peduncle in ♀. Prosartema reaching $\frac{3}{4}$ longitudinal diameter of cornea; stylocerite reaching $\frac{1}{2}$ basal segment peduncle.

Thoracic appendages.—Third maxilliped reaching almost to or to tip of basal segment of antennular peduncle; 1st pereiopod reaching pterygostomial angle; 2nd reaching $\frac{1}{2}$ carpocerite; 3rd reaching as far as eye; 4th reaching base of, 5th reaching as far as or slightly exceeding tip of carpocerite. First and 2nd pereiopods with mastigobranchiae and basial spines, 3rd pereiopods with slightly smaller pair of basial spines in ♂ only.

Abdomen.—Dorsally carinated from anterior 4th somite, carina incised posteriorly on 4th and 5th somites. Sixth somite with 2 pairs faint lateral cicatrices and small horizontal suture at lower $\frac{1}{4}$ posterior edge. Telson unarmed.

Gastric mill (Fig. 26*F*).—Cardiac plate with 32–36 spinules. Zygocardiac ossicle principal teeth + upper row of 5 teeth leading to cluster of about 20 teeth; prepyloric acute with 12–14 teeth on either side.

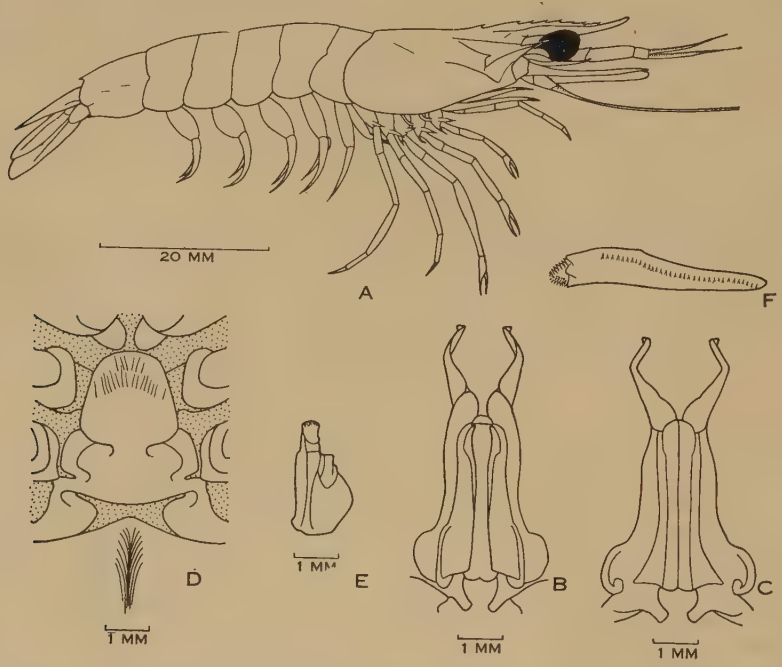

Fig. 26.—*Parapenaeopsis cornutus* (Kishinouye). *A*, 73 mm ♂; *B*, ventral surface of petasma, 73 mm ♂; *C*, dorsal surface of petasma; *D*, thelycum, 81 mm ♀; *E*, appendix masculina; *F*, cardiac plate and zygocardiac ossicle.

Petasma (Fig. 26*B*, *C*).—With a pair of long slender distal projections which diverge and ascend slightly for the proximal $\frac{2}{3}$, distal $\frac{1}{3}$ curving inwards fairly sharply; reaching coxae of 3rd pereiopods and enclosing sharp triangular setose projection on sternal plate of 4th pereiopods. Lateral lobes with a pair of posterior incurving projections, and a pair of large flattened proximolateral projections. Openings of vasa deferentia on either side of a channel leading to triangular sternal plate.

Appendix masculina (Fig. 26*E*).—Appendix masculina 3-segmented. Distal piece with rounded, minutely tuberculate anterodistal rim leading posteriorly to sharp angle. Basal piece thrice length distal piece and penultimate piece together. Endopod of 2nd pleopod shortened, resembling a long boot distally.

Thelycum (Fig. 26*D*).—Anterior plate as wide as long, concave, and with a number of setae across ventral face; with posterior extension fused with posterior plate, on either side of which are a pair of depressions; with prominent median tuft of setae behind the posterior plate.

Colour in life.—Body faintly pinkish with transverse blue bands; uropods proximally red, distally greenish blue; antennal flagella reddish and crossed by broad yellow bands (Kubo 1949).

Distribution

Townsville, Qld.; Ariake-wan, Japan; Java; Takao and Tainan, Formosa (Kubo 1949).

Discussion

This species is apparently an uncommon one. It closely resembles *P. maxillipedo* Alcock, especially thelycum and petasma, but may be distinguished by the following features:

Feature	*P. cornutus*	*P. maxillipedo* (Kubo 1949)
Postrostral carina	Straight, not reaching posterior carapace	Convex, reaching posterior carapace
Rostral teeth	6–7 + epigastric	8–10 + epigastric
Basial spine of 3rd pereiopods ♀	Absent	Present
Cardiac plate	32–36 spinules (41–46 (Kubo 1949))	56–59 spinules

The above description differs from that of Kubo (1949) in the following details:

Feature	Present Description	Kubo (1949)
Transverse groove at $\frac{9}{10}$ carapace in ♂	Absent	Present
Branchiocardiac sulcus	Present in both sexes	Present only in ♂
Prosartema	Reaching $\frac{3}{4}$ eye	Reaching as far as eye
Cardiac plate	32–36 spinules	41–46 spinules
Zygocardiac ossicle	5 teeth on upper row	3 teeth on upper row

As the agreement is otherwise good, the creation of a new species is not justified, especially as differences of the gastric mill armature are the only important ones.

Parapenaeopsis sculptilis (Heller)

Fig. 27*A–G*

Penaeus sculptilis Heller, 1862, p. 528; 1865, p. 122, pl. XI, fig. 1.

Parapenaeopsis sculptilis Kubo, 1949, pp. 389–91.
Parapeneopsis sculptilis var. *cultrirostris* Alcock, 1906, p. 39.
Parapenaeopsis cultrirostris Kubo, 1949, pp. 378–80.

Material.—QUEENSLAND: Keppel Bay, July 1953, 4 ♂, 91–97 mm, 4 ♀, 106–130 mm; Norman River, Gulf of Carpentaria, Aug. 1953, 3 ♂, 53–75 mm, 6 ♀, 59–111 mm.

Description

Rostrum.—Teeth, 6–8, usually 6 + epigastric, latter always feeble, often represented by a barely perceptible depression in ♂ (cf. *Metapenaeus macleayi*). Apparently sexually dimorphic in ♂♂ 70 mm and above, unarmed portion absent,

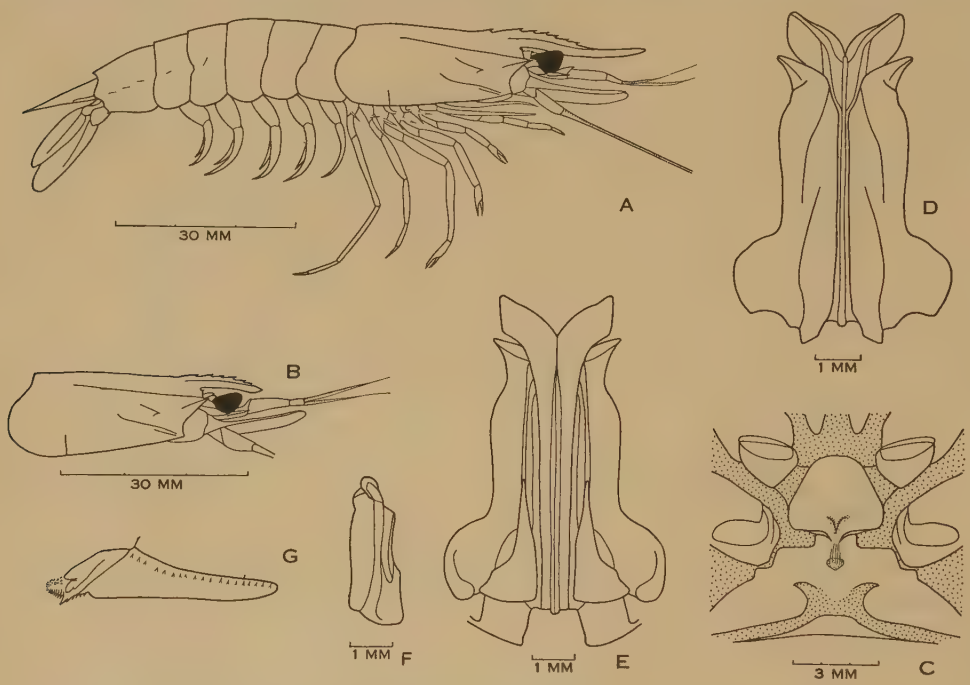

Fig. 27.—*Parapenaeopsis sculptilis* (Heller). *A*, 116 mm ♀; *B*, cephalothorax, 100 mm ♂; *C*, thelycum, 128 mm ♀; *D*, ventral surface of petasma, 97 mm ♂; *E*, dorsal surface of petasma; *F*, appendix masculina; *G*, cardiac plate and zygocardiac ossicle.

rostrum curving downwards, reaching to 2nd segment of antennular peduncle; in ♀ rostrum is long, strongly sigmoidal, unarmed distal $\frac{1}{2}$ strongly upcurved and reaching beyond tip antennular peduncle. (In 53-mm ♂ rostrum is of latter shape.) Epigastric tooth at $\frac{1}{5}$ carapace, 1st tooth at or slightly behind anterior margin of carapace. Postrostral carina low, of uniform height, ending $\frac{1}{20}$ length carapace from posterior end; feebly sulcate, sometimes merely flat-topped, throughout its length and narrowing slightly about the middle. Adrostral carina ending mid way between 1st and 2nd teeth.

Carapace.—Orbital angle small. Longitudinal suture reaching $\frac{3}{4}$ length carapace from postorbital margin, and reaching level of transverse suture. Orbito-antennal

sulcus absent. Antennal spine large, the carina reaching $\frac{1}{2}$ distance between spine and hepatic spine. Cervical sulcus straight, feeble, wide, its upper end indistinct. Hepatic sulcus pronounced, $\frac{1}{3}$–$\frac{1}{2}$ length carapace, inclined downwards at angle of 15° to horizontal, sinuous, posterior end indistinct and curving upwards, ending at $\frac{1}{2}$ carapace at level of hepatic spine; hepatic carina distinct only for lower $\frac{1}{2}$ sulcus, starting below hepatic spine and running towards sharp pterygostomial angle. Feeble indications of a branchiocardiac sulcus usually present.

Antennules.—Flagella subequal, 0·85 length peduncle, and 0·6 length carapace in ♂, and $\frac{3}{4}$ length peduncle and $\frac{1}{2}$ length carapace in ♀. Prosartema reaching tip of junction of peduncle of eye with cornea, stylocerite attaining $\frac{1}{2}$ basal segment.

Thoracic appendages.—Third maxilliped reaching from $\frac{3}{4}$ to slightly exceeding carpocerite; 1st pereiopod reaching from pterygostomial angle, to base of carpocerite; 2nd reaching from base to $\frac{1}{2}$ carpocerite; 3rd reaching from tip to exceeding carpocerite by dactyl; 4th reaching base of, 5th reaching tip of carpocerite. Mastigobranchiae on 1st and 2nd pereiopods, ischial spines absent.

Abdomen.—Dorsally carinated from middle 4th somite, carinae of 4th and 5th ending in angular, sometimes very minutely spinous projections, that of 6th ending in large spine. The 3rd and anterior 4th somites with feeble dorsal sulcus or flat-topped strip indicating its position, often present on 1st and 2nd somites also. Fourth somite with 1, 5th with 1, 6th with 3 pairs of faint lateral cicatrices. Telson unarmed.

Gastric mill (Fig. 27*G*).—Cardiac plate with 17–21 spinules. Zygocardiac ossicle 3 principal + upper row of 7–8 smaller and lower cluster of about 25 teeth; 5 teeth on edge of cardiac plate; prepyloric with 9–12 lateral teeth.

Petasma (Fig. 27*D*, *E*).—Reaching basis of 4th pereiopods, with pair apical spout-like projections directed anterolaterally and opening ventrally, distance between their apices almost equal that of distolateral projections, which is $\frac{2}{5}$ total length petasma. Petasma constricted at 0·7 its length; a pair of very large prominent lateral proximal projections, slightly curved dorsally, ending posteriorly in knob-like processes.

Appendix masculina (Fig. 27*F*).—Distal piece with expanded, flattened distolateral region inclined at 45° to longitudinal axis and $\frac{1}{5}$ length basal piece.

Thelycum (Fig. 27*C*).—Anterior plate slightly concave, length 0·7–0·8 width; with 2 low tubercles on posterior edge separated by shallow median depression and articulating with corresponding pair of tubercles on rectangular posterior sternal plate, latter with tubercle bearing tuft of setae.

Colour (*freshly preserved*).—Four wide whitish transverse bands, evenly spaced along carapace and abdomen, edged with narrow pink bands, region between white and pink bands light to dark brown; appendages pink to red.

Distribution

Keppel Bay to Gulf of Carpentaria, Qld.; Indonesia, Singapore, Hong Kong, Gulf of Martaban, Bombay (Kubo 1949). Abundance in commercial quantities has been reported for Keppel Bay.

Discussion

Burkenroad (1934*b*) does not regard the shorter rostrum of ♂ as being even a variant of normal form, but "an adult instar ultimately attained by all males". While ♀♀ often seem to have damaged rostra, this apparently being a feature of slender, long rostra generally, none examined were as short as those of ♂♂, which seem to have been derived by the unarmed portion being broken off close to the last tooth. Tips of all ♂ rostra were variable and appeared slightly malformed. Alcock (1906) states that the unarmed portion is often lost, and presumably had examined intact adult ♂♂. It may be that ♂, just before reaching adult instar, is for some reason more likely to suffer rostral damage, possibly because ♂ rostrum is less robust than that of ♀.

Kubo (1949) elevates *P. sculptilis* var. *cultrirostris* to *P. cultrirostris* but it is significant that Kubo did not examine any ♂ *P. sculptilis* nor any ♀ *P. cultrirostris*. The description of the latter agrees well with that of ♂♂ described above. Position of epigastric tooth, sulcation of postrostral carina and 1st and 2nd abdominal somites, appear to be variable and therefore not valid for creating a distinct species.

Parapenaeopsis venusta de Man

Fig. 28

Parapenaeopsis venusta de Man, 1907, p. 134; 1911, pp. 93–5, pl. IX, fig. 30.

Material.—QUEENSLAND: Albany Passage, Cape York, Sept. 1928, coll. M. Ward, ♀, 45 mm.

Description

Rostrum.—Teeth 7 + epigastric. Rostrum slightly exceeding 1st antennular segment, distal $\frac{1}{3}$ free portion curving slightly ventrad, extreme tip upturned. Adrostral carina ending just behind 1st tooth; postrostral carina ending at $\frac{1}{2}$ carapace. Epigastric 0·36 length carapace, 1st tooth on carapace. Greatest depth of rostrum just in front of 2nd tooth.

Carapace.—Postocular sulcus present. Orbital angle not spinous. Longitudinal suture ending just behind level of hepatic spine, transverse suture at tip of coxae of 3rd pereiopods. Upper edge of antennal spine forming a right angle with border of carapace; carina not extending behind edge of carapace. Hepatic spine slender; cervical sulcus $\frac{1}{7}$ length carapace, slightly inclined upwards. Hepatic sulcus extending horizontally for $\frac{1}{2}$ length behind hepatic spine, its anterior $\frac{1}{2}$ inclined downwards towards pterygostomial angle. Hepatic carina along anterior $\frac{1}{2}$ sulcus, anterior edge with row of spinous setae. Pterygostomial angle sharp.

Antennules.—Flagella subequal and 0·8 length peduncle and $\frac{1}{2}$ length carapace. Stylocerite $\frac{1}{3}$ length 1st segment; prosartema reaching as far as tip of junction of peduncle of eye with cornea.

Thoracic appendages.—Third maxillipeds much stouter than pereiopods and reaching $\frac{1}{2}$ 2nd segment of antennular peduncle; 1st pereiopod reaching base of, 2nd reaching tip of carpocerite, 3rd exceeding it by dactyl; 4th reaching $\frac{1}{2}$ and 5th exceeding carpocerite by dactyl. No ischial spines and mastigobranchiae on pereiopods.

Abdomen.—Fifth and 6th somites dorsally carinated. Telson with 4 small lateral movable spines, most distal largest. Distal and penultimate spines close together, distance separating them less than $\frac{1}{2}$ that separating remaining 2.

Thelycum (Fig. 28).—Anterior plate mucronate, $\frac{2}{3}$ as long as wide, not including posterior extension. Posterior $\frac{1}{2}$ concave, concavity extending along a posterior extension, which lies in a rectangular incision of posterior plate. Distolateral extensions of posterior plate flat, enclosing posterior $\frac{1}{3}$ anterior plate; a transverse depression occupying middle region of posterior plate.

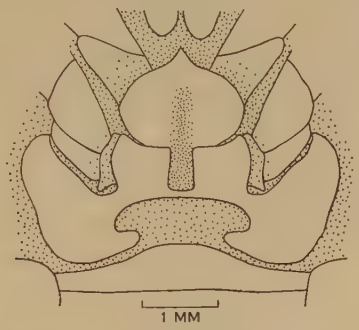

Fig. 28.—*Parapenaeopsis venusta* de Man. Thelycum, 45 mm ♀.

Distribution

So far known only from the type locality (13 m, east coast of Aru Is.) and from Albany Passage.

Discussion

The present specimen agrees in most respects with de Man's (1911) description, except that the anterior plate of thelycum is wider than that shown in de Man's figure.

The integument of the Albany Passage specimen is very soft and damaged, making it unsuitable for figuring. However, absence of mastigobranchiae on 1st and 2nd pereiopods, presence of an epigastric tooth, short rostrum and longitudinal suture, enables *P. venusta* to be readily separated from other species of the genus. ♂ is still unknown.

Parapenaeopsis tenellus (Bate)

Fig. 29*A–G*

Penaeus tenellus Bate, 1888, pp. 270–1. Kishinouye, 1900, p. 22.
Penaeus curcifer Ortmann, 1890, p. 451.
Penaeus (*Parapenaeopsis*) *tenellus* de Man, 1907, pp. 435–6, 454.
Parapenaeopsis tenella de Man, 1911, pp. 9, 92.
Parapenaeopsis tenellus Kubo, 1949, pp. 371–4.

Material.—QUEENSLAND: Townsville, 20 fm, Aug. 1953, ♀, 44 mm; mouth Norman R., Gulf of Carpentaria, Aug. 1953, 2 ♂, 32 mm, 2 ♀, 36, 37 mm.

Description

Rostrum.—Teeth 6–8, epigastric absent; reaching almost to tip of 2nd segment of antennular peduncle, proximal $\frac{1}{3}$ rising from carapace, remainder more or less horizontal, tip with slight upward curve. Adrostral carina ending at $\frac{1}{4}$ carapace, postrostral carina broad, indistinct posteriorly, ending at $\frac{1}{2}$ carapace; 1st tooth at edge of carapace.

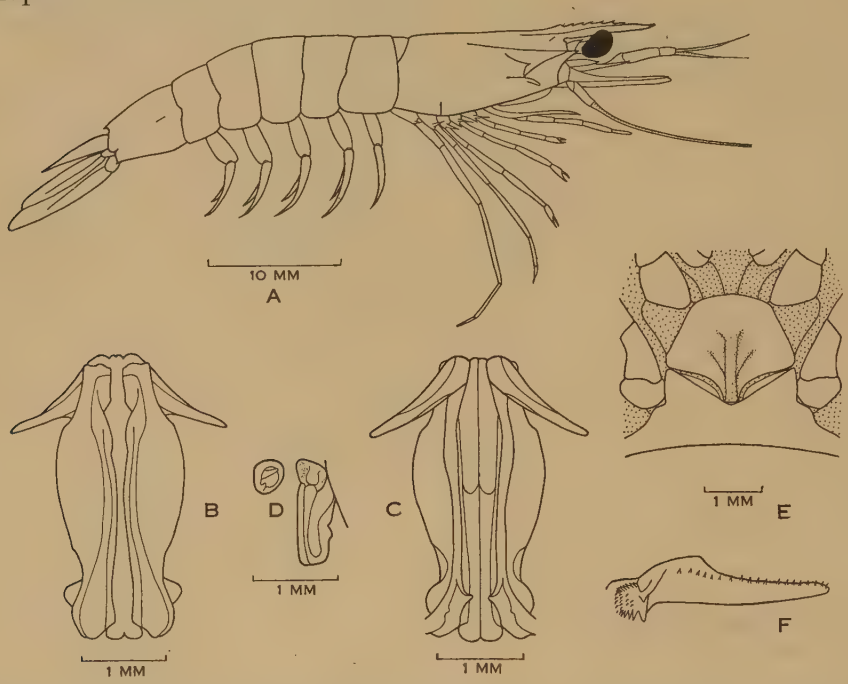

Fig. 29.—*Parapenaeopsis tenellus* (Bate). *A*, 44 mm ♀; *B*, ventral surface of petasma, 32 mm ♂; *C*, dorsal surface of petasma; *D*, appendix masculina and end view of distal piece; *E*, thelycum, 44 mm ♀; *F*, cardiac plate and zygocardiac ossicle.

Carapace.—Minutely punctate, with acute orbital angle and a postocular sulcus. Longitudinal suture reaching $\frac{2}{3}$ carapace from anterior edge. Antennal spine large, carina indistinct, occupying anterior $\frac{1}{4}$ distance between antennal and hepatic spines. Cervical sulcus feeble, wide, and reaching almost to longitudinal suture. Hepatic sulcus almost horizontal posteriorly, anterior $\frac{1}{2}$ inclined downwards towards acute pterygostomial angle; hepatic carina along anterior $\frac{1}{2}$ sulcus only.

Antennules.—Flagella subequal, equal to length peduncle and 0·8 carapace in ♂, 0·7–0·8 peduncle and 0·5 carapace in ♀. Prosartema reaching tip of junction of optic peduncle with cornea; stylocerite reaching $\frac{1}{2}$ basal segment.

Thoracic appendages.—Third maxillipeds reaching as far as or slightly exceeding basal segment of antennular peduncle; 1st pereiopod exceeding pterygostomial angle by dactyl; 2nd reaching $\frac{1}{2}$ carpocerite; 3rd reaching base of dactyl of 3rd maxillipeds; 4th reaching as far as tip of 1st, 5th reaching as far as tip of 2nd segment of antennular peduncle. No mastigobranchiae on 1st and 2nd pereiopods.

Abdomen.—Dorsally carinated from 4th somite. Exopods uropods $1\frac{1}{2}$ times length unarmed telson. Sixth somite with horizontal anterior lateral cicatrice, and horizontal suture on lower $\frac{1}{4}$ posterior edge.

Gastric mill (Fig. 29*F*).—Cardiac plate with 16–21 teeth. Zygocardiac ossicle 3 principal + upper row of about 6, and lower row of 3–4 teeth, and total of 15–20 in 4 vertical rows between ends of these rows. Prepyloric acute with 8–10 lateral teeth, most median 3–5 large and prominent.

Petasma (Fig. 29*B*, *C*).—Reaching basis of 3rd pereiopods, distolateral projections of lateral lobes slender, tapering, and reflected posterolaterally, making angle of 60° with longitudinal axis of petasma; distance between tips of projections $\frac{4}{5}$ total length petasma. Lateral lobes expanded laterally into elongate keeled projections, their length, and also distance across their most lateral extremities, $\frac{1}{2}$ length petasma. Peduncle of pleopod with mediodistal process, consisting of proximal sharp tubercle and distal larger, blunter tubercle.

Appendix masculina (Fig. 29*D*).—Distal piece broad, minutely setose, $\frac{1}{3}$ length basal piece, with posterodistal excavation with tongue-like process, and with tubercle on anterior rim of excavation.

Thelycum (Fig. 29*E*).—Anterior plate $1\frac{1}{2}$ times as wide as long, with median groove occupying posterior $\frac{2}{3}$; with a posterior tongue-like projection enclosed by large flat anterior processes of posterior plate, and with an accessory ridge on each side of front of posterior plate.

Distribution

Townsville and Norman River, Gulf of Carpentaria, Qld. Southern half of Japan (Kubo 1949).

Discussion

The above description is in close agreement with that of Kubo (1949) except that Kubo states that a postocular sulcus is absent. All specimens examined had a distinct, though shallow, postocular sulcus, and it is possible this was overlooked by Kubo, whose description was mainly based on 1 female.

P. tenellus is one of the 4 *Parapenaeopsis* spp. which lack mastigobranchiae on 1st and 2nd pereiopods, the others being *P. hungerfordi* Alcock, *P. venusta* de Man, and *P. acclivirostris* Alcock. Of these only the last lacks an epigastric tooth and is closely similar to *P. tenellus*. However, in *P. acclivirostris* the antennular flagella are $\frac{1}{2}$ length peduncle, and anterior plate of thelycum wants a posterior tongue-like extension, according to Alcock (1906). Both species are very small penaeids (♂ *P. tenellus* mature at 30 mm, ♀ 40 mm), and this may account for their apparent rarity and discontinuous distribution.

IV. Zoogeographical Distribution

The majority of Penaeinae are restricted to tropical and warm-temperate shallow seas, being most abundant in the former. Little collecting has been done in northern Australia and adjacent areas. There are few records from New Guinea and from most of the Pacific islands. There are a number of records from northern Queensland

and north-western Australia, but except for a few specimens from Darwin the region between these areas has been almost entirely neglected. Nevertheless, in spite of these shortcomings it is possible to integrate the zoogeography of the Australian Penaeinae. Of 28 species described above, 17 are considered in this respect. Five new species, with *Funchalia villosa*, *Metapenaeopsis borradailei*, *M. durus*, *M. mogiensis*, *Trachypenaeus granulosus*, and *Parapenaeopsis venusta*, comprise the remainder and are omitted from subsequent discussion.

(*a*) *Australian Distribution* (*Table* 1)

A cool-temperate Australian penaeinine fauna is virtually non-existent. Prawns are absent from the cold Maugean Province (as defined by Bennett and Pope (1953)), and *Penaeus latisulcatus* and *Metapenaeopsis novae-guineae* are rare in South Australia and confined to sheltered inlets (Hale 1927). Only *Penaeus plebejus* and *Metapenaeus macleayi* are not found in tropical waters and are confined to the region corresponding roughly to the Peronian Province (Bennett and Pope 1953). Decreasing temperature, in the vicinity of Twofold Bay (D. Rochford, personal communication), probably limits the southern distribution of these two species. On the other hand, *Penaeus plebejus* and *Metapenaeus macleayi* do not extend far into Queensland waters. This may be explained by regarding them as endemic Australian species. This is in accord with the general principle that species peculiar to Australia are found only in the colder southern regions (Bennett and Pope (1953), rocky shores; various authors quoted by them; Thomson (1947), chaetognaths; Thompson (1948), pelagic tunicates; Munro (1949), silver bream; Kott (1952), ascidians; Stephenson and McNeill (1955), stomatopods). As such species are lacking in the Penaeinae, it is likely that any endemic Australian species would be found in the adjacent warm-temperate Peronian Province. Stephenson and McNeill (1955) record one endemic species for this region. Thomson (1947) did not find any tropical species of chaetognath further south than 38° S. latitude (approximately Cape Howe) and Kott (1952) found the southern limit for tropical ascidians to be Sydney. It seems likely, therefore, that if endemic Australian species have evolved from typically tropical animal groups, they would be restricted to the Peronian Province.

Apart from *Penaeus plebejus* and *Metapenaeus macleayi*, only *M. endeavouri* and *Trachypenaeus anchoralis* are not also recorded outside Australian waters. It is likely that these species will be found in Indonesia, as *Penaeus esculentus*, while most common in Australian waters, has recently been recorded from Borneo (Kubo 1949). In addition to these four species, *P. latisulcatus*, *P. semisulcatus*, *P. merguiensis*, *Metapenaeopsis novae-guineae*, and *Trachypenaeus fulvus* are found across northern Australia. It is probable that further collecting will show a similar distribution for the widely ranging *Penaeus monodon*, *Metapenaeus monoceros*, *Trachypenaeus curvirostris*, and *Parapenaeopsis sculptilis*. The two remaining *Parapenaeopsis* spp. are rare as yet and predictions concerning their distribution cannot be made.

Thus in the Penaeinae there is little to substantiate the division of tropical and subtropical Australia into a Banksian Province, extending inside the Great Barrier Reef from Cape York to approximately Wide Bay, and a Dampierian Province from Geraldton to Cape York (Bennett and Pope 1953). A similar situation has been

found for chaetognaths (Thomson 1947), ascidians (Kott 1952), stomatopods (Stephenson and McNeill 1955), portunid crabs (Stephenson, unpublished data), and the dominant littoral molluscs and barnacles (Endean, Kenny, and Stephenson 1956; Endean, Stephenson, and Kenny 1956). Clark (1946) found it convenient to erect a division of the echinoderm fauna at Cape York, but admits to the paucity of records west of the Cape. It is probable that the proximity of Cape York to New Guinea is responsible for the concept of some kind of geographical barrier in this region, whereas most faunal evidence to date is to the contrary.

TABLE 1
DISTRIBUTION OF 17 PENAEIDAE WITHIN AUSTRALIA
? indicates probable occurrence

Species	N.S.W.	S. Qld.	N. Qld.	N.T.	W.A.	S.A.
Penaeus plebejus	+	+				
P. latisulcatus			+	+	+	+
P. monodon		+	+	?	+	
P. esculentus	+	+	+	+	+	
P. semisulcatus	+	+	+			
P. merguiensis	+	+	+	+	+	
Metapenaeopsis novae-guineae	+	+	+	+	+	+
Metapenaeus monoceros	+	+	+	?	+	
M. endeavouri	+	+	+	+	+	
M. mastersii	+	+	+	+	+	
M. macleayi	+	+				
Trachypenaeus curvirostris	+	+	?	?		
T. fulvus	+	+	+	+	+	
T. anchoralis		+	+	+	+	
Parapenaeopsis cornutus			+			
P. sculptilis			+			
P. tenellus			+			

(*b*) *Indo–West Pacific Distribution* (*Fig.* 30)

The tropical and subtropical oceans inhabited by the Penaeinae can be subdivided into three regions:

(i) The Atlantic and Mediterranean,

(ii) Pacific America,

(iii) Indo–West Pacific.

Each has a discrete fauna, none of the species in a given region so far being recorded from another, though the Suez and Panama Canals are possible avenues of migration from one region to another (Monod 1930). Most of the species of Penaeinae are found in the Indo–West Pacific.

The distribution and abundance of Penaeinae shown in Figure 30 indicates that Australian species of the subfamily are very largely a southern extension of the

Indonesian fauna. The two exceptions are *Penaeus plebejus* and *Metapenaeus macleayi* as noted above. Clark (1946) arrived at the same conclusion for echinoderms, and Stephenson and McNeill (1955) for stomatopods. This situation is to be expected in view of Australia's geographical position, with the continental shelf extending northwards into Indonesia.

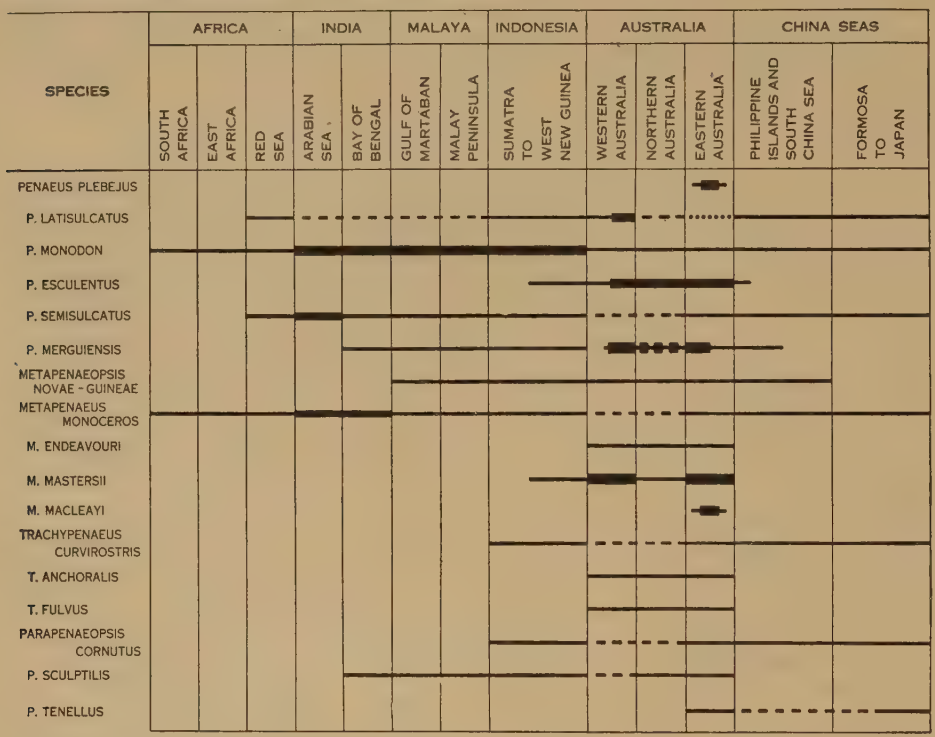

Fig. 30.—Indo–West Pacific distribution of 17 Australian Penaeinae. Heavy lines, commercial abundance; unbroken lines, recorded in the literature, but abundance not stated; broken lines, occurrence probable, but no actual record; dotted lines, present but rare.

In Figure 30 it can be seen that some species have very wide distribution while others are curiously restricted. *Penaeus latisulcatus* ranges from the Red Sea to Japan, and occurs in Western Australian waters in commercial quantities, but is rare on the east coast. The very closely related *P. plebejus*, on the other hand, is found only on the east coast where it is commercially abundant. Another example of one species breaking the distribution of another is shown by *P. esculentus* and *P. monodon*. The former occurs in commercial abundance across northern Australia, whereas the latter, which has an extremely wide distribution in large numbers, is not abundant on the east coast and probably will be found sparsely scattered on the north and west coasts of Australia. There is also the possibility of a similar relationship existing between the wide-ranging *Metapenaeus monoceros* and *Metapenaeus endeavouri*, though the abundance of the latter in northern Australia is unknown. In the Atlantic *Penaeus brasiliensis* Latreille is widely distributed but does not occur in the Gulf of Mexico, where the closely related *P. duoarum* Burkenroad and *P. aztecus*

Ives are found (Anderson and Lindner 1945). However, the two latter differ from *P. plebejus* in having a range similar to that of *P. brasiliensis*. The existence of some sort of mutual exclusion between certain penaeid species therefore seems possible. Summarizing the zoogeography of Australian Penaeinae, it is possible to state that:

(1) There are two endemic species, the southern limits of which are probably determined by hydrographical conditions, and the northern limits of which may be determined by either ecological or hydrographical factors, or a combination of both.

(2) The rest of the Australian species are a southern extension of the Indonesian fauna.

(3) Certain abundant species may interrupt the distribution of otherwise widely ranging closely related species elsewhere abundant.

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List of Species

Genus *Atypopenaeus* (Alcock)

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M. mogiensis (Rathbun) 172
M. novae-guineae (Haswell) 170
M. sinuosus, sp. nov. 176

Genus *Metapenaeus* Wood-Mason & Alcock

M. eboracensis, sp. nov. 193
M. endeavouri (Schmitt) 187
M. macleayi (Haswell) 196
M. mastersii (Haswell) 190
M. monoceros (Fabricius) 184

Genus *Parapenaeopsis* (Alcock)

P. cornutus (Kishinouye) 215
P. sculptilis (Heller) 217
P. tenellus (Bate) 221
P. venusta de Man 220

Genus *Parapenaeus* Smith

P. australiensis, sp. nov. 179

Genus *Penaeus* Fabricius

P. caesius, sp. nov. 143
P. esculentus Haswell 157
P. latisulcatus Kishinouye 149
P. merguiensis de Man 160
P. monodon Fabricius 152
P. plebejus Hess 147
P. semisulcatus de Haan 154

Genus *Trachypenaeus* (Alcock)

T. anchoralis (Bate) 209
T. curvirostris (Stimpson) 203
T. fulvus, sp. nov. 206
T. granulosus (Haswell) 211

THE BIOGEOGRAPHY OF QUEENSLAND'S SHALLOW-WATER ECHINODERM FAUNA (EXCLUDING CRINOIDEA), WITH A REARRANGEMENT OF THE FAUNISTIC PROVINCES OF TROPICAL AUSTRALIA

By R. Endean*

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Summary

Analysis of Queensland's shallow-water echinoderm fauna reveals that approximately 44 per cent. of the 267 species recorded are confined to Queensland mainland waters and approximately 35 per cent. to Barrier Reef waters; the remainder are common to both environments.

Marked faunistic attenuation with increasing latitude is exhibited by echinoderms occurring on the mainland north of lat. 25° S. and also by those found on the Great Barrier Reef. In both cases there are few substitutions. South of lat. 25° S. Peronian species occur, but an apparently isolated population of tropical species is found in the Moreton Bay–Caloundra area.

Queensland mainland echinoderms have strong affinities with those of the East Indies. The principal exchange route utilized by mainland species common to both areas seems to be via Torres Strait and the Arafura Sea. The Coral Sea appears to present a barrier to the spread of mainland species to the West Pacific area.

On the other hand Barrier Reef echinoderms have strong ties with those of the latter region. Gene flow between populations of species common to the Barrier Reef and the West Pacific area probably occurs by way of the Coral Sea as a result of the transport of the pelagic larval stages of West Pacific populations by the Pacific south equatorial current. A dearth of coral structures immediately to the west of Torres Strait seems to have prevented the spread of Barrier Reef species to northern Australian waters. However, a few reef echinoderms appear to have entered north-western Australian waters from the East Indies, probably by way of atolls and reef platforms found on the Sahul and Rowley Shelfs.

The echinoderm fauna of north-western Australia contains a large number of endemic species but has marked affinities with those of East Indian and Queensland mainland waters.

The origin of the echinoderm fauna of tropical Australia is discussed in the light of palaeogeographic and zoogeographic findings. It is concluded that the present fauna of the area is derived predominantly from recent East Indian and West Pacific stocks. Also it is postulated that barriers between echinoderm populations present in tropical Australian waters were set up during the Pleistocene falls of sea-level and that this has resulted in the formation of closely allied sympatric and allopatric species.

Available evidence indicates that the Solanderian Province should be restricted to the Great Barrier Reef area and, since Torres Strait does not present a barrier to the dispersal of echinoderms typically found in habitats in which terrigenous sediments predominate, the fauna of Queensland mainland waters and that of the Dampierian Province are grouped together tentatively in a single Tropical Australian Province.

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I. Introduction

Thanks to the work of H. L. Clark, the specific composition and general distribution of Australia's echinoderms are now reasonably well known. He has shown (Clark 1946) that there is a predominance of tropical species which he believed had their origins in regions to the north of Australia. In 1921 he put forward much evidence in support of his contention that the present echinoderm fauna of the Queensland coast has resulted from the mixing of immigrant species from the Pacific Ocean with East Indian species which have entered Queensland waters via Torres Strait.

However, Endean (1953) noted that the echinoderm fauna of Port Curtis (a mainland locality) differed markedly from that of Heron I. and Lady Musgrave I.—coral cays near the southern tip of the Barrier Reef. Later (Endean 1956), it was noted that the bulk of species occurring on coral structures along the Great Barrier Reef were rarely found on the shores of the Queensland mainland, whilst species common in mainland waters seemed to be restricted to muddy, sandy, stony, or gritty habitats. This suggests that Great Barrier Reef and mainland echinoderms may represent two distinct stocks which have not intermingled to any great extent.

Clark (1946) agreed with Hedley on the limits of the Australian marine faunistic provinces. Hedley (1904, 1926) had recognized four faunistic provinces on the Australian coast. On the eastern coast Hedley delineated the "Solanderian Province" as the area extending from Torres Strait to Wide Bay (about 26° S.) and the "Peronian Province" as the region from Wide Bay to eastern Victoria. The region from Bass Strait west and north to Geraldton in Western Australia he termed the "Adelaidean Province" (later changed to Flindersian by Cotton (1930)), and the remaining sector of the Australian coast—the region from Geraldton to Cape York—the "Dampierian Province".

Subsequently Whitley (1932) proposed that the term "Solanderian" be restricted to the fauna of the Great Barrier Reef and that the name "Banksian" be given to the fauna of the Queensland coast proper. Clark (1946) either ignored or overlooked Whitley's proposal, for he stated (p. 467) that "the Solanderian province is essentially the Great Barrier Reef area, extending from the Murray Is. in the north to Lady Elliott Island in the south, but it includes as well, very naturally, the coastal fauna of Queensland from Cape York southward".

However, Endean, Kenny, and Stephenson (1956) considered that the junction between the Solanderian and Peronian Provinces should be re-located at about lat. 25° S., and in a later paper (Endean, Stephenson, and Kenny 1956) put forward evidence which, to some extent, supported Whitley's proposal.

If Clark's work on Australian echinoderms be used as a basis, recent information obtained on the distribution of Queensland species (Endean 1953, 1956) sheds new light on the biogeography of these species and on the delineation of Queensland's faunistic provinces.

II. The Queensland Echinoderm Fauna

Table 1 includes all well-authenticated species (excluding crinoids) that have been recorded from waters of less than 20 fm off the Queensland coast. New species

can still be expected from Queensland but there is no reason to believe that the discovery of these will alter radically the conclusions reached in this paper. Owing to the author's unfamiliarity with the Crinoidea this class is excluded from the present discussion.

Species occurring only on reefs of the Great Barrier Reef or on coral islands off the coast are designated "reef" species, whilst species found elsewhere in Queensland waters are regarded as "mainland" species. It will be noted that some species occur in both reef and mainland waters.

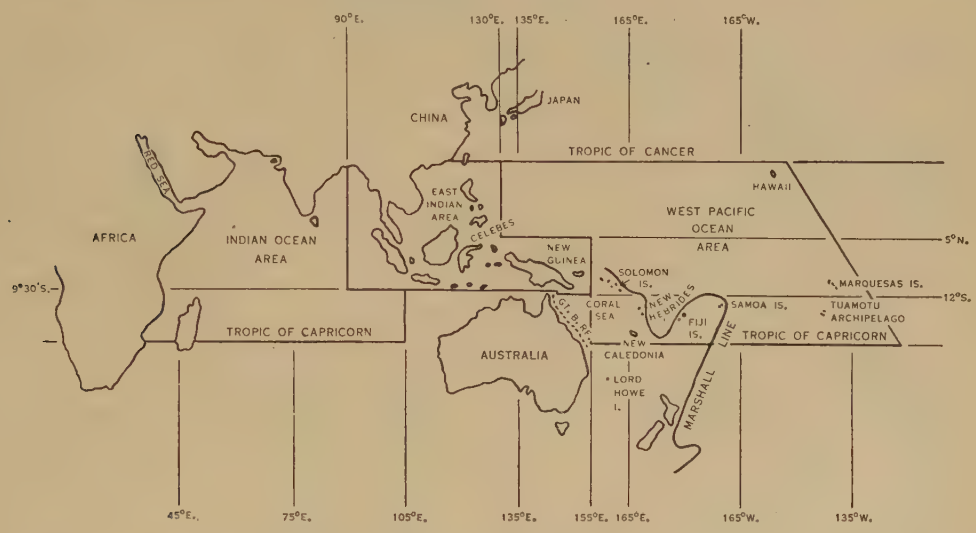

Fig. 1.—The Indo–West Pacific region, showing biogeographical areas mentioned in the text.

Owing to a lack of ecological data uncertainty has arisen regarding the designation of many species recorded from continental islands off the coast. Since the intertidal fauna of these islands has been shown to be closely allied to that of the mainland (Endean, Stephenson, and Kenny 1956) such species are regarded as mainland species.

For the purposes of this paper the geographical limits of the East Indies are based on those fixed by Clark (1946). The tropical region to the east of the East Indies–Australian area, stretching as far as Hawaii, the Marquesas Is., and the Tuamotu Archipelago, is here referred to as the West Pacific Ocean area, whilst the region to the west of the East Indies–Australian area as far as the east coast of Africa and the Red Sea is here termed the Indian Ocean area. The boundaries of these geographical areas are shown on Figure 1, and localities within Australia on Figure 2.

One species, *Clypeaster australasiae* (Gray), is recorded by Clark (1946) from Brisbane Water, Queensland. It is believed that the record should be Brisbane Water, N.S.W., as there is no locality of that name to be found in Queensland.

III. Existence of "Mainland" and "Reef" Elements in Fauna

Analysis of the species list in Table 1, which comprises 267 echinoderm species belonging to 128 genera, reveals that 112 have not been recorded from the Great

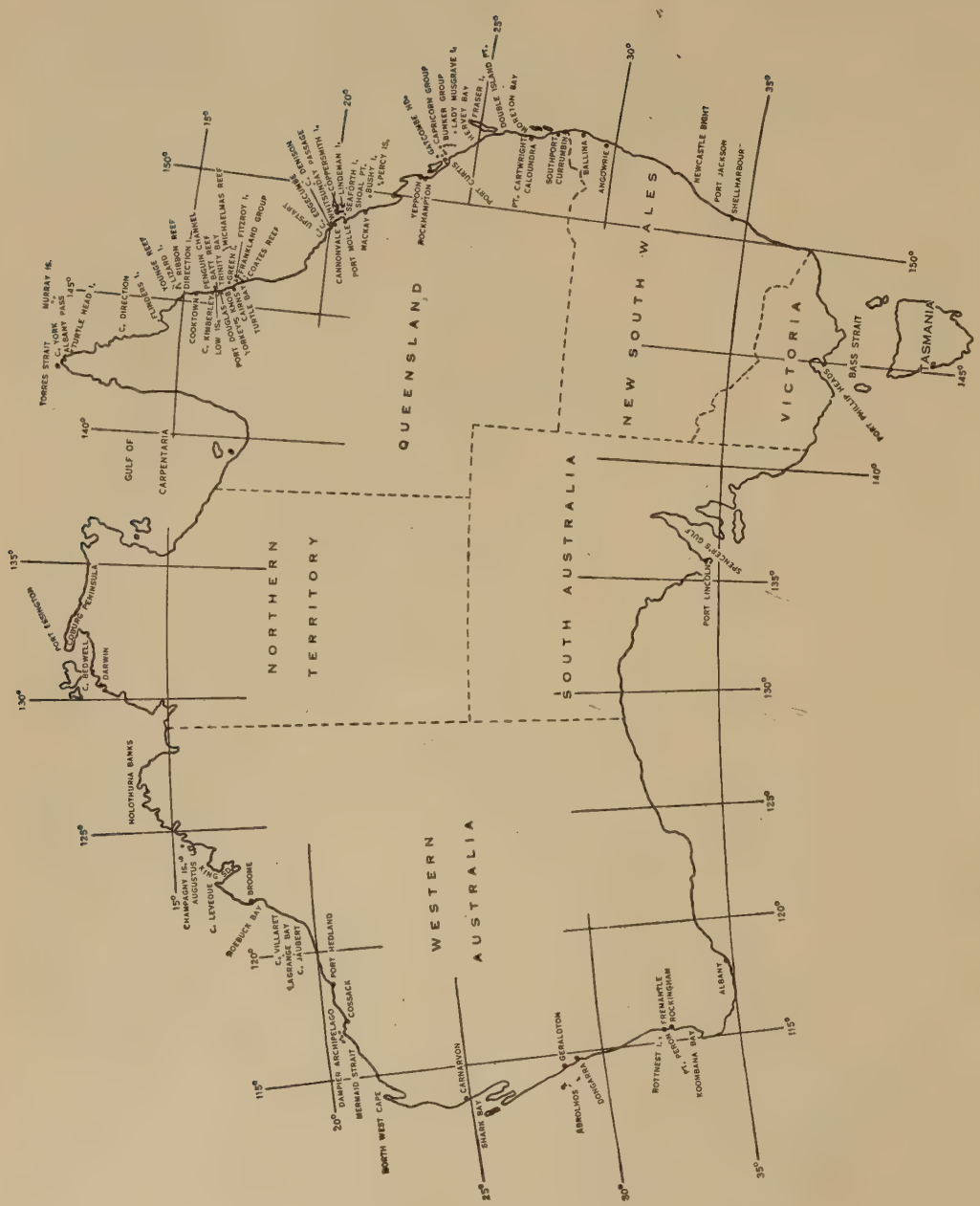

Fig. 2.—Australia, showing localities where echinoderm species mentioned in the text have been recorded.

TABLE 1

THE DISTRIBUTION OF LITTORAL ECHINODERMS FOUND IN QUEENSLAND WATERS

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA					
LUIDIIDAE					
**Luidia australiae* Doderlein	Moreton Bay S. to Vic. and around southern shores of Australia to Fremantle, W.A.				
**Luidia forficifera* Sladen	Torres Strait S. to Newcastle Bight, N.S.W.		×	×	
ASTROPECTINIDAE					
**Astropecten granulatus* Muller & Troschel	Torres Strait S. to Hervey Bay and W. around northern half of the continent to Fremantle, W.A.				
Astropecten monacanthus Sladen	Gulf of Carpentaria W. to Broome, W.A.		×	×	
**Astropecten polyacanthus* Muller & Troschel	Torres Strait S. to Port Jackson, N.S.W.		×	×	×
**Astropecten vappa* Muller & Troschel	Probably right around Australia				
ARCHASTERIDAE					
**Archaster typicus* Muller & Troschel	Torres Strait S. to Lindeman I. and W. to Coburg Pensinsula, N.T.	Low Isles		×	×
GONIASTERIDAE					
Mediaster praestans Livingstone		Barrier Reef near Cairns			
**Goniodiscaster coppingeri* (Bell)	Torres Strait S. to Port Curtis and W. to Cape Bedwell, N.T.				
**Goniodiscaster integer* Livingstone	Lindeman I.; Port Curtis; Moreton Bay				
Goniodiscaster pleyadella (Lamarck)	Torres Strait			×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
Pseudogoniodiscaster wardi Livingstone	Port Curtis				
Tosia queenslandensis Livingstone		Low Isles; Capricorn Group			
Iconaster longimanus (Mobius)	Torres Strait S. to Percy Isles and W. to Broome, W.A.			×	
**Stellaster incei* Gray	Torres Strait S. to Moreton Bay and W. around tropical Australia to Lagrange Bay, W.A.		×	×	
Stellaster princeps Sladen	Torres Strait W. around northern Australia to Port Hedland, W.A.				
**Anthenea acanthodes* Clark	Port Curtis				
**Anthenea acuta* (Perrier)	Fraser I. S. to Tasmania				
**Anthenea aspera* Doderlein	Port Curtis				
**Anthenea crassa* Clark	Port Curtis				
Anthenea mertoni Koehler	Gulf of Carpentaria W. around shores of N.T.			×	
OREASTERIDAE					
**Protoreaster nodosus* (L.)	Torres Strait S. to Mackay**	Murray Is. S. to Low Isles	×	×	×
**Pentaceraster australis* (Lutken)	Lizard I. S. to Moreton Bay				
Pentaceraster gracilis (Lutken)	Torres Strait to SE. of Lady Musgrave I. and W. around tropical Australia to Lacépède Is., W.A.			×	
**Culcita novaeguineae* Muller & Troschel		Murray Is. S. to Capricorn Group; Augustus I., W.A.	×	×	×
ASTEROPIDAE					
**Asterope carinifera* (Lamarck)	Fitzroy I.	Murray Is. S. to Low Isles	×	×	×
**Petricia vernicina* (Lamarck)	Caloundra S. and W. to Spencer's Gulf, S.A.				

* In collection of Zoology Department, University of Queensland. **Unpublished record.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
METRODIRIDAE					
**Metrodira subulata* Gray	Torres Strait S. to Moreton Bay and W. to Carnarvon, W.A.		×	×	
OPHIDIASTERIDAE					
Fromia elegans Clark		Murray Is. S. to Coates Reef; Abrolhos, W.A.			
**Fromia milleporella* (Lamarck)		Murray Is. S. to Bunker Group	×	×	×
Nardoa mollis de Loriol		Murray Is.	×	×	
**Nardoa novaecaledoniae* (Perrier)		Murray Is. S. to Bunker Group		×	×
**Nardoa pauciforis* (von Martens)		Murray Is. S. to Bunker Group		×	×
**Nardoa rosea* Clark		Murray Is. S. to Capricorn Group			
**Neoferdina ocellata* (Clark)		Murray Is. S. to Capricorn Group			×
**Linckia guildingii* Gray		Younge and Ribbon Reefs S. to Bunker Group; Broome, W.A.	×	×	×
**Linckia laevigata* (L.)		Murray Is. S. to Bunker Group	×	×	×
Bunaster uniserialis Clark		Murray Is.			
Leiaster speciosus von Martens		Murray Is.		×	
Ophidiaster armatus Koehler	Lindeman I.			×	
**Ophidiaster confertus* Clark	Fraser I. S. to Shellharbour, N.S.W.	Capricorn Group			
**Ophidiaster granifer* Lutken		Murray Is. S. to Bunker Group		×	×
Ophidiaster lioderma Clark		Murray Is.			
Ophidiaster propinquus Livingstone		Ribbon Reef			
Ophidiaster squameus Fisher		Murray Is.		×	×
**Ophidiaster watsoni* Livingstone	Bushy I., off Mackay	Capricorn Group			

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
Hacelia helicosticha (Sladen)	Torres Strait W. to Holothuria Bank, W.A.				
Tamaria fusca Gray	Off Direction I.			×	
Tamaria megaloplax (Bell)	Torres Strait W. to Broome, W.A.	Snake Reef	×	×	
ASTERINIDAE					
Asterina anomala Clark		Murray Is.; Cape Leveque, W.A.			×
**Asterina burtonii* Gray		Murray Is. S. to Bunker Group; Roebuck Bay, Shark Bay, and the Abrolhos, W.A.	×	×	×
**Asterina nuda* Clark	Caloundra	Murray Is.			
**Patiriella calcar* (Lamarck)	Currumbin S. to Tas. and W. to Spencer's Gulf, S.A.				
**Patiriella exigua* (Lamarck)	Torres Strait S. to Tas. and W. to Spencer's Gulf, S.A.	Murray Is. S. to Low Isles	×	×	×
Disasterina abnormalis Perrier		Murray Is. S. to Michaelmas Cay, off Cairns			×
**Disasterina leptalacantha* (Clark)		Capricorn Group			
Disasterina praesignis Livingstone	Port Curtis				
**Nepanthia belcheri* (Perrier)	Yeppoon S. to Port Jackson, N.S.W.				
**Nepanthia brevis* (Perrier)	Torres Strait S. to Port Curtis and W. to Darwin, N.T.				
Tegulaster emburyi Livingstone		Capricorn Group			
**Anseropoda rosacea* (Lamarck)	Fraser I.; Broome and Port Hedland, W.A.	Capricorn Group	×	×	
ECHINASTERIDAE					
Echinaster acanthodes Clark	Off Fraser I.				
**Echinaster luzonicus* (Gray)	Torres Strait S. to Fraser I.	Murray Is. S. to Bunker Group		×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ASTEROIDEA (*Continued*)					
ACANTHASTERIDAE					
Acanthaster planci (L.)		Murray Is. S. to Low Isles	×	×	×
VALVASTERIDAE					
Valvaster spinifera Clark		Murray Is.			
PTERASTERIDAE					
**Retaster insignis* Sladen	Torres Strait S. to Moreton Bay and W. around northern Australia to Shark Bay, W.A.			×	
OPHIUROIDEA					
OPHIOMYXIDAE					
**Ophiomyxa australis* Lutken	Off Lizard I. S. to Tas. and W. around southern Australia to between Geraldton and Fremantle, W.A.	Low Isles S. to Bunker Group	×	×	×
TRICHASTERIDAE					
**Euryale aspera* Lamarck	Torres Strait S. to Double I. Point and W. around tropical Australia to Cape Villaret, W.A.			×	
Astrobrachion adhaerens (Studer)	Port Molle; Whitsunday Passage; off "north-western Australia"				
GORGONOCEPHALIDAE					
Astrocladus granulatus Clark	Lindeman I.				
Astrochalcis tuberculosus Koehler	Albany Passage			×	
OPHIACANTHIDAE					
Ophiacantha discoidea Lyman		Murray Is.		×	
Ophiacantha gracilis (Studer)		Murray Is.; "north of Dampier Archipelago", W.A.			
Ophiacantha tenuispina Clark	Off Gatcombe Head, Port Curtis				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
AMPHIURIDAE					
Amphiura bidentata Clark	Port Curtis; Broome, W.A.				
Amphiura constricta Lyman	Probably right around Australia				
Amphiura diacritica Clark	Black I., Whitsunday Passage				
Amphiura microsoma Clark		Murray Is.; Broome and Rottnest I., W.A.			
Amphiura septemspinosa Clark		Murray Is.; Cape Bedwell, N.T.			
Ophiocentrus dilatatus (Koehler)		Murray Is.; Darwin		×	
Ophionephthys octacantha Clark	Torres Strait; Broome, W.A.				
**Amphipholis squamata* (Delle Chiaje)	Probably right around Australia	Probably right along the Barrier Reef	×	×	×
Amphiodia ochroleuca (Brock)	Probably right around Australia			×	
Amphioplus depressus (Ljungman)	Torres Strait W. around tropical Australia to Point Peron, W.A.		×	×	×
Amphioplus parviclypeus Clark	Torres Strait				
Ophiactis acosmeta Clark	Port Curtis; Broome, W.A., W. and S. to Rockingham, W.A.				
Ophiactis delicata Clark		Murray Is.			
Ophiactis hemiteles Clark		Murray Is.			
Ophiactis luteomaculata Clark		Murray Is.; off Ballina, N.S.W.; Broome, W.A.			
Ophiactis modesta Brock	Torres Strait W. to Broome, W.A.		×	×	×
**Ophiactis savignyi* (Muller & Troschel)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Fremantle, W.A.	Murray Is. S. to Bunker Group	×	×	×
OPHIOTRICHIDAE					
**Ophiothrix acestra* Clark	Port Curtis S. to Shellharbour, N.S.W.	Low Isles			
**Ophiothrix caespitosa* Lyman	Caloundra S. around southern Australia and N. to Shark Bay, W.A.				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
**Ophiothrix exigua* Lyman	Torres Strait S. to Port Curtis and W. to Broome, W.A.			×	×
Ophiothrix stelligera Lyman	Torres Strait W. around tropical Australia to Koombana Bay, W.A.	Murray Is.	×	×	×
Amphiophiothrix demessa (Lyman)		Murray Is.	×	×	×
**Macrophiothrix longipeda* (Lamarck)	Torres Strait S. to Moreton Bay and W. around northern Australia to Broome, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Macrophiothrix megapoma Clark	Cape York S. to Penguin Channel				
Macrophiothrix rhabdota (Clark)		Murray Is.		×	
Macrophiothrix rugosa Clark		Murray Is.			
**Placophiothrix lineocaerulea* (Clark)	Moreton Bay; Broome, W.A.				
Placophiothrix melanosticta (Grube)	Torres Strait W. around northern Australia to Port Hedland, W.A.			×	
**Placophiothrix spongicola* (Stimpson)	Currumbin S. around southern coasts of Australia to Dongarra and the Abrolhos, W.A.				
Placophiothrix striolata (Grube)	Torres Strait S. to Lindeman I.			×	
Placophiothrix trilineata (Lutken)		Murray Is. S. to Bott Reef, near Cairns		×	×
Placophiothrix virgata (Lyman)		Murray Is.		×	×
**Ophiothela hadra* Clark	Torres Strait S. to Ballina, N.S.W., and W. around tropical Australia to Albany, W.A.	Murray Is.			
Ophiotrichoides irregularis Clark	Port Curtis				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiotrichoides liodisca (Clark)		Murray Is.		×	
**Ophiotrichoides martensi* (Lyman) *australis* (Clark)	Torres Strait S. to Port Curtis and W. around tropical Australia to Cossack, W.A.	Murray Is.			
**Ophiotrichoides nereidina* (Lamarck)	Lizard I. S. to Fraser I.	Murray Is. S. to Capricorn Group		×	
Ophiotrichoides propinqua (Lyman)		Murray Is.	×	×	×
Ophiomaza cacaotica Lyman	Torres Strait S. to Port Curtis and W. around tropical Australia to Broome, W.A.	Murray Is.	×	×	×
Ophiomaza cataphracta (Brock)	Cape York				
Ophiomaza obscura (Ljungman)		Murray Is.; "north-west Australia"	×	×	×
Ophiogymna lineata Clark	W. of Low Isles				
OPHIOCHITONIDAE					
Ophionereis lineata Clark	Lindeman I.				
Ophionereis porrecta Lyman		Murray Is.	×	×	×
**Ophionereis semoni* (Doderlein)	Torres Strait S. to Lindeman I. and W. around northern Australia to Broome, W.A.	Low Isles		×	
Ophionereis tigris Clark		Capricorn Group			
OPHIOCOMIDAE					
**Ophiocoma brevipes* Peters	Green I.	Murray Is. S. to Bunker Group	×	×	×
**Ophiocoma erinaceus* Muller & Troschel		Murray Is. S. to Capricorn Group	×	×	×
**Ophiocoma insularia* Lyman *variegata* Smith		Murray Is. S. to Capricorn Group; Abrolhos, W.A.			

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiocoma parva Clark		Murray Is.; Port Essington, N.T.; Cape Leveque and Rottnest I. W.A.			
**Ophiocoma pica* Muller & Troschel		Murray Is. S. to Low Isles	×	×	×
Ophiocoma schoenleinii Muller & Troschel	Lindeman I.; Frankland Group	Murray Is.		×	×
**Ophiocoma scolopendrina* (Lamarck)		Murray Is. S. to Bunker Group	×	×	×
Ophiomastix annulosa (Lamarck)		Murray Is. S. to Ellison Reef		×	
**Ophiomastix asperula* Lutken		Murray Is. S. to Low Isles		×	×
Ophiomastix bispinosa Clark	Lizard I.				×
Ophiomastix caryophyllata Lutken		Murray Is.		×	×
Ophiomastix corallicola Clark		Murray Is.			
Ophiomastix flaccida Lyman		Murray Is.		×	
Ophiomastix janualis Lyman		Murray Is.		×	
**Ophiomastix mixta* Lutken	Frankland Group	Murray Is. S. to Low Isles		×	×
**Ophiarthrum elegans* Peters	Torres Strait S. to Lindeman I. and W. around northern Australia to Augustus I., W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Ophiarthrum pictum* (Muller & Troschel)	Lindeman I.	Murray Is. S. to Low Isles		×	×
OPHIODERMATIDAE					
**Ophiarachna incrassata* (Lamarck)		Murray Is. S. to Capricorn Group	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
OPHIUROIDEA (*Continued*)					
Ophiarachna megacantha Clark	Lindeman I.				
Ophiopezella spinosa (Ljungman)	Torres Strait	Murray Is.		×	×
Ophiochasma stellatum (Ljungman)	Torres Strait S. to Lindeman I.; Broome, W.A.			×	
**Ophiarachnella gorgonia* (Muller & Troschel)	Torres Strait S. to Cairns and W. around tropical Australia to Port Hedland, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Ophiarachnella infernalis* (Muller & Troschel)	Torres Strait S. to Port Molle and W. around northern Australia to Broome, W.A.	Murray Is. S. to Low Isles		×	
**Ophiarachnella septemspinosa* (Muller & Troschel)		Murray Is. S. to Bunker Group; Augustus I., W.A.	×	×	×
Cryptopelta granulifera Clark	Off Lizard I.		×		
OPHIOLEPIDIDAE					
Ophiura kinbergi Ljungman		Murray Is.; Port Jackson, N.S.W., S. to Bass Strait and W. to Spencer's Gulf, S.A.; Broome, W.A.	×	×	×
Ophioteichus multispinum Clark	Lindeman I.				
Ophiolepis cincta Muller & Troschel	Torres Strait	Murray Is.	×	×	×
Ophiolepis nodosa Duncan	Frankland Group			×	
**Ophiolepis superba* Clark	Torres Strait S. to Port Douglas and W. to Darwin, N.T.	Murray Is. S. to Capricorn Group	×	×	×
**Ophioplocus imbricatus* (Muller & Troschel)		Murray Is. S. to Capricorn Group; Darwin, N.T.; Broome, Shark Bay, and the Abrolhos, W.A.	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA					
CIDARIDAE					
Phyllacanthus imperialis (Lamarck)	Torres Strait	Murray Is.	×	×	×
**Phyllacanthus parvispinus* Tenison Woods	Point Cartwright S. to Tas.				
Prionocidaris australis (Ramsay)	Fraser I. S. to Bass Strait				
Prionocidaris bispinosa (Lamarck)	Torres Strait S. to Port Denison and W. around northern Australia to Shark Bay and the Abrolhos, W.A.		×	×	
Prionocidaris verticillata (Lamarck)		Low Isles	×	×	×
CENTRECHINIDAE					
**Diadema setosum* (Leske)	Torres Strait S. to Moreton Bay; Augustus I. and the Abrolhos, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Diadema savignyi* Michelin		Murray Is. S. to Capricorn Group; Abrolhos, W.A.	×	×	×
**Echinothrix calamaris* (Pallas)		Murray Is. S. to Capricorn Group	×	×	×
**Echinothrix diadema* (L.)		Murray Is. S. to Capricorn Group	×	×	×
Astropyga radiata (Leske)	Torres Strait, Double I. Point		×	×	×
ECHINOTHURIIDAE					
Asthenosoma intermedium Clark	Seaforth I., near Mackay				
STOMOPNEUSTIDAE					
**Stomopneustes variolaris* (Lamarck)	Trinity Bay to Port Denison	Murray Is. S. to Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
TEMNOPLEURIDAE					
**Temnopleurus alexandri* (Bell)	Torres Strait S. to Port Jackson and W. to Broome, W.A.			×	
**Temnopleurus toreumaticus* (Leske)	From 15° S. on Qld. coast to Moreton Bay; Gulf of Carpentaria		×	×	×
Salmacis belli Doderlein	Torres Strait S. to Lindeman I. and W. to Holothuria Bank, W.A.			×	
**Salmacis sphaeroides* (L.)	Torres Strait S. to Port Jackson, N.S.W., and W. to Broome, W.A.	Low Isles		×	
Temnotrema bothryoides (Agassiz & Desor)	Torres Strait W. around tropical Australia to King Sound, W.A.			×	
Temnotrema siamense (Mortensen)	Torres Strait; Holothuria Bank, W.A.	Murray Is.	×	×	
Mespilia globulus (L.)	Trinity Bay; Augustus and Champagny Is., W.A.			×	×
ECHINIDAE					
Cyrtechinus verruculatus (Lutken)	Green I.		×	×	×
**Nudechinus darnleyensis* (Tenison Woods)	Torres Strait S. to Moreton Bay and W. around tropical Australia to Cape Jaubert, W.A.				
Nudechinus multicolor (Yoshiwara)		Low Isles, Three Isles		×	
**Tripneustes gratilla* (L.)	Moreton Bay S. to Port Jackson, N.S.W.; Shark Bay and the Abrolhos, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Gymnechinus epistichus Clark	Torres Strait S. to Port Denison			×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
STRONGYLOCENTROTIDAE					
**Echinostrephus molaris* (de Blainville)		Murray Is. S. to Low Isles	×	×	×
**Echinostrephus aciculatus* Agassiz		Capricorn Group		×	×
**Heliocidaris erythrogramma* (Valenciennes)	Caloundra S. around southern shores of Australia to Shark Bay and the Abrolhos, W.A.				
**Heliocidaris tuberculata* (Lamarck)	Caloundra** S. to Port Jackson, N.S.W.				
ECHINOMETRIDAE					
Parasalenia gratiosa Agassiz	Green I.; Augustus and Champagny Is., W.A.	Murray Is.	×	×	×
**Echinometra mathaei* (de Blainville)	Torres Strait S. to Moreton Bay; Shark Bay, the Abrolhos, and Rottnest I., W.A.	Murray Is. S. to Bunker Group	×	×	×
**Heterocentrotus mammillatus* (L.)		Murray Is. S. to Capricorn Group; "north-west Australia"	×	×	×
CLYPEASTRIDAE					
**Clypeaster telurus* Clark	Torres Strait S. to Southport and W. around tropical Australia to Fremantle, W.A.				
**Arachnoides placenta* (L.)	Torres Strait S. to Moreton Bay and W. around northern Australia to Augustus and Champagny Is., W.A.			×	×
LAGANIDAE					
**Laganum depressum* Agassiz	Torres Strait	Low Isles S. to Capricorn Group	×	×	×
Peronella lesueuri (Agassiz)	Torres Strait S. to Port Molle and W. around tropical Australia to Fremantle, W.A.			×	

* In collection of Zoology Department, University of Queensland. **Unpublished record.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
Peronella orbicularis (Leske)	Torres Strait S. to Cape Upstart and W. around tropical Australia to Shark Bay, W.A.			×	
Peronella peronii (Agassiz)	"Southern Queensland" S. to Tas.				
FIBULARIIDAE					
Fibularia volva Agassiz & Desor	Torres Strait W. to Cape Jaubert, W.A.		×	×	×
SCUTELLIDAE					
Echinodiscus tenuissimus (Agassiz & Desor)	Torres Strait			×	×
ECHINONEIDAE					
**Echinoneus cyclostomus* Leske		Murray Is. S. to the Capricorn Group	×	×	×
HEMIASTERIDAE					
Schizaster lacunosus (L.)	Torres Strait; Turtle I.		×	×	
**Moira lethe* Mortensen	Probably right around Australia				
SPATANGIDAE					
Metalia spatagus (L.)	Torres Strait	Low Isles	×	×	×
Metalia sternalis (Lamarck)		Low Isles; Port Essington, N.T.	×	×	×
**Rhynobrissus hemiasteroides* Agassiz	Shoal Point S. to Moreton Bay; Broome, W.A.				×
**Brissus latecarinatus* (Leske)	Torres Strait; Port Jackson, N.S.W.; Port Essington, N.T.; Port Lincoln, S.A.	Murray Is. S. to Capricorn Group	×	×	×
**Maretia planulata* (Lamarck)	Cooktown S. to Port Jackson, N.S.W.	Low Isles	×	×	×
**Breynia australasiae* (Leach)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Fremantle and the Abrolhos, W.A.				
Lovenia elongata (Gray)	Lindeman I.; Broome, W.A.		×	×	

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
ECHINOIDEA (*Continued*)					
Echinocardium cordatum (Pennant)	Flinders I.; Port Jackson, N.S.W.; Tas.		×	×	×
HOLOTHURIOIDEA					
CUCUMARIIDAE					
Cucumaria semperi Bell	Torres Strait S. to Port Denison and W. around northern Australia to Broome, W.A.			×	
Pentacta australis (Ludwig)	Probably right around Australia				
**Pentacta cucumis* (Semper)	Torres Strait S. to Coppersmith I.			×	
Pentacta minuta (Ludwig)	Off Low Isles, Port Denison; Albany, W.A.				
**Pentacta quadrangularis* (Troschel)	Lizard I. S. to Moreton Bay; Broome, W.A., W. and S. to Albany, W.A.			×	
**Pentacta tuberculosa* (Quoy & Gaimard)	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Shark Bay, W.A.			×	
**Pseudocolochirus axiologus* (Clark)	Mackay; Augustus I. W. to Cape Jaubert, W.A.				
**Acolochirus challengeri* (Theel)	Torres Strait S. to Moreton Bay			×	
Pentathyone mirabilis (Ludwig)	Torres Strait S. to Port Curtis and W. around tropical Australia to Shark Bay, W.A.				
**Thyone buccalis* Stimpson	Torres Strait S. to Port Jackson, N.S.W., and W. around tropical Australia to Shark Bay, W.A.		×	×	
**Thyone papuensis* Theel	Torres Strait S. to Moreton Bay and W. around tropical Australia to Mermaid Strait, W.A.				

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
Actinocucumis difficilis Bell	Torres Strait W. to Broome, W.A.				
Actinocucumis typicus Ludwig	Torres Strait S. to Port Denison and W. around tropical Australia to Shark Bay, W.A.				
**Discucumaria africana* (Semper)	Torres Strait S. to Caloundra and W. to "north-western Australia"	Murray Is. S. to Bunker Group	×	×	
Pseudocucumis aciculus (Semper)		Murray Is.	×	×	×
**Mensamaria intercedens* (Lampert)	Torres Strait S. to Moreton Bay and W. around tropical Australia to King Sound, W.A.			×	
Phyllophorus proteus Bell	Torres Strait S. to Port Molle and W. to Broome, W.A.				
Phyllophorus trapezus Clark	Off Cape Kimberley	Low Isles			
**Urodemas schmeltzii* (Ludwig)	Torres Strait S. to Moreton Bay and W. around northern Australia to Cape Jaubert, W.A.				
STICHOPODIDAE					
**Stichopus chloronotus* Brandt	Torres Strait	Murray Is. S. to Bunker Group	×	×	×
**Stichopus horrens* Selenka	Torres Strait S. to Moreton Bay	Murray Is. S. to Low Isles		×	×
**Stichopus variegatus* Semper	Torres Strait; Broome, W.A., W. and S. to "south-western Australia"	Murray Is. S. to Bunker Group	×	×	×
Thelenota ananas (Jaeger)		Murray Is.		×	×
HOLOTHURIIDAE					
**Labidodemas semperianum* Selenka		Murray Is. S. to Capricorn Group	×	×	×
Holothuria albiventer Semper	Off Direction I.; Carnarvon, W.A.		×		
**Holothuria arenicola* Semper	Port Denison S. to Moreton Bay	Murray Is. S. to Bunker Group	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Holothuria argus* (Jaeger)	Cooktown	Murray Is. S. to Bunker Group	×	×	×
**Holothuria atra* Jaeger	Caloundra; Augustus I., W.A.	Murray Is. S. to Bunker Group	×	×	×
Holothuria axiologa Clark		Murray Is.			
**Holothuria coluber* Semper	Torres Strait	Murray Is. S. to Low Isles		×	
**Holothuria difficilis* Semper	Caloundra; "West Australia"	Murray Is. S. to Capricorn Group	×	×	
**Holothuria edulis* Lesson		Murray Is. S. to Capricorn Group	×	×	×
**Holothuria erinaceus* Semper	Shoal Point, Cape Edgecumbe	Low Isles		×	×
**Holothuria fuscocinerea* Jaeger	Torres Strait S. to Port Denison	Murray Is. S. to Low Isles	×	×	×
**Holothuria fusco-olivacea* Fisher		Low Isles			×
**Holothuria impatiens* (Forskål)	Torres Strait S. to Caloundra and W. around tropical Australia to Shark Bay, W.A.	Murray Is. S. to Bunker Group	×	×	×
Holothuria inhabilis Selenka		Murray Is.		×	×
**Holothuria leucospilota* (Brandt)	Torres Strait S. to Angowrie, N.S.W., and W. around tropical Australia to Shark Bay, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Holothuria marmorata* (Jaeger)		Murray Is. S. to Capricorn Group; Broome, W.A.	×	×	×
**Holothuria martensii* Semper	Torres Strait S. to Cannonvale	Murray Is.	×	×	
**Holothuria modesta* Ludwig	Torres Strait S. to Port Curtis and W. around northern Australia to Cape Jaubert, W.A.		×	×	×
**Holothuria moebii* Ludwig	Mackay; Yorkey's Knob		×	×	×
**Holothuria monacaria* Lesson	Torres Strait W. to Cape Leveque, W.A.	Murray Is. S. to Capricorn Group	×	×	×
Holothuria notabilis Ludwig	Port Denison	Low Isles		×	
**Holothuria ocellata* (Jaeger)	Torres Strait to Moreton Bay			×	
**Holothuria paradoxa* Selenka		Low Isles			×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Holothuria pardalis* Selenka	Torres Strait S. to Moreton Bay and W. around northern Australia to Broome, W.A.	Murray Is. S. to Capricorn Group	×	×	×
**Holothuria pervicax* Selenka		Murray Is. S. to Bunker Group; Shark Bay, W.A.	×	×	×
Holothuria remollescens Lampert		Murray Is.	×		
Holothuria rigida (Selenka)	Turtle Bay, Green I.	Murray Is.	×	×	×
Holothuria rugosa Ludwig		Murray Is.		×	×
**Holothuria scabra* Jaeger	Torres Strait S. to Moreton Bay	Low Isles S. to Capricorn Group	×	×	×
**Holothuria verrucosa* Selenka		Murray Is. S. to Low Isles	×	×	×
Actinopyga echinites (Jaeger)	Torres Strait S. to Port Denison and W. around tropical Australia to Shark Bay, W.A.		×	×	×
Actinopyga lecanora (Jaeger)	Torres Strait W. to Broome, W.A.	Murray Is.	×	×	×
**Actinopyga mauritiana* (Quoy & Gaimard)		Murray Is. S. to Bunker Group	×	×	×
**Actinopyga miliaris* (Quoy & Gaimard)	Torres Strait; "Western Australia"	Murray Is. S. to Low Isles	×	×	×
MOLPADIIDAE					
**Paracaudina australis* (Semper)	Rockhampton, Mackay; various localities in S.A.				
SYNAPTIDAE					
Euapta godeffroyi (Semper)	Torres Strait	Murray Is.	×	×	×
Opheodesoma grisea (Semper)	Torres Strait S. to Port Denison	Murray Is.	×	×	
**Polyplectana kefersteinii* (Selenka)		Murray Is. S. to Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

TABLE 1 (*Continued*)

Species	Australian Range of "Mainland Species"	Australian Range of "Reef Species"	Indian Ocean Area	East Indies Area	West Pacific Area
HOLOTHURIOIDEA (*Continued*)					
**Synapta maculata* (Chamisso & Eysenhardt)		Murray Is. S. to Low Isles	×	×	×
Chondrocloea nigra (Semper)		Murray Is.		×	
**Chondrocloea recta* (Semper)	Torres Strait S. to Moreton Bay and W. around tropical Australia to Shark Bay, W.A.	Low Isles	×	×	×
CHIRIDOTIDAE					
**Chiridota rigida* Semper	Moreton Bay	Murray Is. S. to Capricorn Group		×	
**Polycheira rufescens* (Brandt)	Cape York S. to Port Denison	Low Isles	×	×	×

* In collection of Zoology Department, University of Queensland.

Barrier Reef or from localities where corals are a dominant element in the fauna. Indeed these 112 echinoderms appear to be restricted to mainland coastal waters and to the waters around the continental islands.

An additional 6 species (*Archaster typicus*, *Ophiothrix acestra*, *Ophionereis semoni*, *Salmacis sphaeroides*, *Maretia planulata*, and *Polycheira rufescens*) are very common in mainland waters, and in Queensland have been recorded from only one coral-dominated locality—Low Isles. As Low Isles is relatively close to the mainland (about 7 miles distant) and since the species listed occur there on the sand flat or amongst rubble, these species can be regarded as species which have strayed into the coral environment (see Endean 1956).

Thus 118 or approximately 44 per cent. of the total number of echinoderm species found in Queensland waters are essentially mainland species.

Of the total Queensland species 85 appear to be confined to coral-dominated areas. An additional 9 (*Asterope carinifera*, *Ophiocoma brevipes*, *Ophiomastix mixta*, *Ophiarthrum pictum*, *Stichopus chloronotus*, *Holothuria argus*, *Holothuria atra*, *Holothuria difficilis*, and *Chiridota rigida*) have each been recorded from only a single mainland locality but are very common in Barrier Reef waters. Thus 94 or approximately 35 per cent. of Queensland echinoderms are essentially reef species.

There remain 55 species, or 21 per cent. of the total, which occur both in coral-dominated and in mainland waters. Some species are not well known, and eventually may be found to belong to one or other of the preceding categories. However, the majority appear to be just as common in Barrier Reef waters as in mainland coastal waters.

IV. Faunistic Attenuation with Increasing Latitude

(*a*) *Species Found in Mainland Waters North of Lat.* 25° *S.*

Figure 3 illustrates the attenuation with increasing latitude of tropical echinoderms occurring in eastern Queensland mainland waters. (Species which range right around Australia have been excluded.)

The majority of species considered range from Torres Strait southward for various distances but some endemic species have been found only in restricted regions along the coast. Also some species found on the east coast of Queensland have not been recorded from the Torres Strait region although they occur in extra-Australian regions further north or on the Australian mainland coast to the west. It is a reasonable assumption that such species occur in Torres Strait but have been overlooked. They are:

Amphiura bidentata, *Anseropoda rosacea*, *Astrobrachion adhaerens*, *Cryptopelta granulifera*, *Cyrtechinus verruculatus*, *Echinocardium cordatum*, *Holothuria albiventer*, *H. arenicola*, *H. erinaceus*, *H. moebii*, *H. notabilis*, *H. rigida*, *Lovenia elongata*, *Maretia planulata*, *Mespilia globulus*, *Ophiactis acosmeta*, *Ophiocoma schoenleinii*, *Ophiolepis nodosa*, *Ophiomyxa australis*, *Ophionereis nereidina*, *Parasalenia gratiosa*, *Pentacta quadrangularis*, *Placophiothrix lineocaerulea*, *Pseudocolochirus axiologus*, *Rhynobrissus hemiasteroides*, *Stomopneustes variolaris*, *Tamaria fusca*, *Temnopleurus toreumaticus*.

Of the 19 asteroids recorded from, or (*Anseropoda rosacea*, *Tamaria fusca*) believed to occur in, Torres Strait (Fig. 3*a*), 4 have not been found to the south. All but 1 of the remainder occur to at least lat. 20° S., 10 still further to the biogeographical boundary at about lat. 25° S., and 3 into New South Wales waters. There are 5 asteroids endemic to the Port Curtis region and 1 to the Lindeman I. area, and 1 has been taken only from the vicinity of Lizard I. In addition *Pentacer-aster australis* appears to be confined to the area between Lizard I. and Moreton Bay, *Goniodiscaster integer* to that between Lindeman I. and Moreton Bay, and

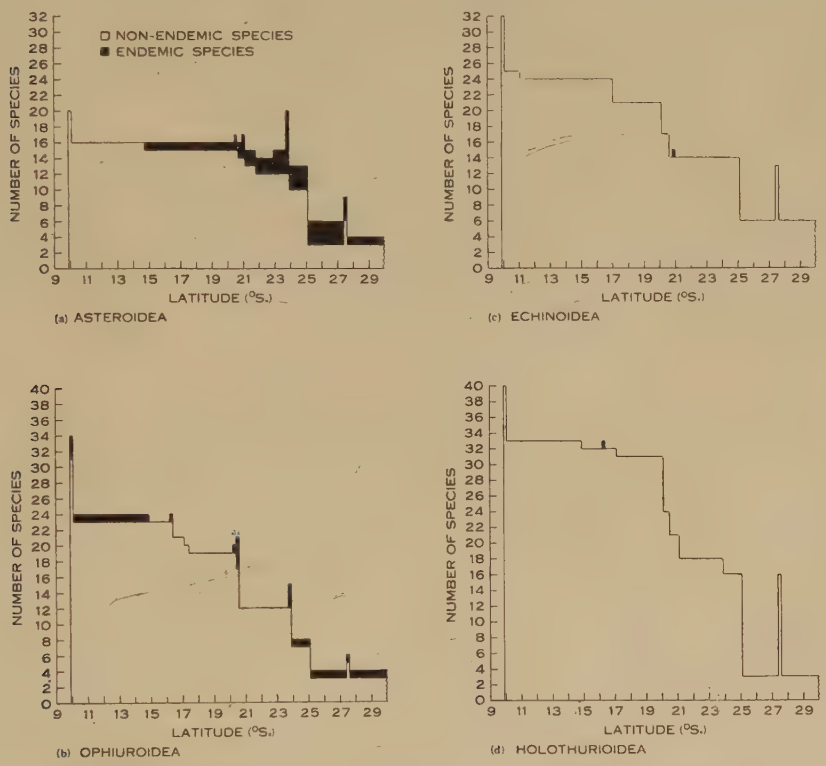

Fig. 3.—Distribution of mainland echinoderm species with latitude.

Nepanthia belcheri to the region between Yeppoon and Port Jackson, N.S.W. The last-named may be a southern species.

Of the ophiuroids, 34 species probably occur in Torres Strait (Fig. 3*b*); 24 of these have extended their ranges to the south. At lat. 20° S. 19 are represented but at the biogeographical boundary at lat. 25° S. only 7 occur. Several ophiuroids seem to be endemic to certain restricted localities along the coast. *Ophiothrix acestra* ranges from Port Curtis to Port Jackson, N.S.W., and is possibly a Peronian species which has extended its range to the north of the biogeographical boundary.

Of the 32 echinoids which have been recorded from or thought to occur in Torres Strait, 7 have not been recorded to the south, 19 extend southwards along

the Queensland coast, and the remaining 6 range south along the New South Wales coast (Fig. 3*c*). Only 1 species, *Asthenosoma intermedium*, seems to be endemic to mainland waters.

Holothurians are well represented in Queensland mainland waters (Fig. 3*d*). A total of 40 species probably occur in the Torres Strait region, 31 of these range as far south as lat. 20° S., and 16 occur in Moreton Bay. Only 3 species, however, range into New South Wales waters.

In general it would appear that the majority of echinoderm species occurring in eastern Queensland mainland waters range from Torres Strait southwards at least as far as lat. 20° S. Between this parallel and the biogeographical boundary at lat. 25° S. a marked decline in the number of species representing each class other than the Asteroidea occurs. Of the asteroids a number of endemic species are found between lat. 20° and 25° S.

Only a few of the species commonly found in mainland waters to the north of the biogeographical boundary have extended their ranges far into the Peronian Province. However, Moreton Bay (about 100 miles to the south of the biogeographical boundary) appears to be a haven for tropical echinoderms (see Endean 1953) as it is for many of the other animal groups commonly found on the coastline of tropical Queensland (Endean, Kenny, and Stephenson 1956).

(*b*) *Species Found in Barrier Reef Waters*

Figure 4 shows the number of species of each echinoderm class (excluding the crinoids) occurring in the Murray Is., the Low Isles, and the Capricorn–Bunker Group regions. These are the sole regions where "reef" echinoderms have been collected intensively in Queensland waters. However, they are conveniently placed for discussion of the faunistic attenuation with increasing latitude in Barrier Reef waters.

Although at the Murray Is. there are more species of ophiuroids than asteroids, echinoids, or holothurians, the numbers of ophiuroid species are markedly fewer to the south of that region. Along the greater part of the Barrier Reef the holothurians seem to be richer in species than any other group. Apart from *Echinometra mathaei*, *Echinostrephus molaris*, *E. aciculatus*, and *Diadema setosum*, echinoids are not well represented in Barrier Reef waters.

Of the 25 asteroids found at the Murray Is. (Fig. 4*a*) 11 range along the entire length of the Barrier Reef and 6 to the vicinity of Low Isles, whilst 8 (4 of which seem to be endemic) do not appear to range south. *Nardoa rosea* seems to be endemic to the Barrier Reef area. *Asterina nuda* has been recorded only from the Murray Is. and Caloundra. As Caloundra is south of the Barrier Reef area, this species is considered to range along the whole length of the Great Barrier Reef. *Tosia queenslandensis* has been recorded only from Low Isles and the Capricorn Group. *Disasterina leptalacantha* and *Tegulaster emburyi* appear to be confined to the Capricorn Group. *Ophidiaster watsoni* has been recorded only from the Capricorn Group and from Lindeman I.; and although *Anseropoda rosacea* has been recorded only from Fraser I. and the Capricorn Group, it occurs in waters to the north of Australia and presumably

extends right along the Queensland coast north of lat. 25° S.; but whether as a reef or a mainland species or as one common to both environments is not known. It has been omitted from Figure 4*a*.

Of interest is the occurrence of the Peronian asteroid *Ophidiaster confertus* at the Capricorn Group, since this appears to be the only instance of a Peronian species extending its range into Barrier Reef waters.

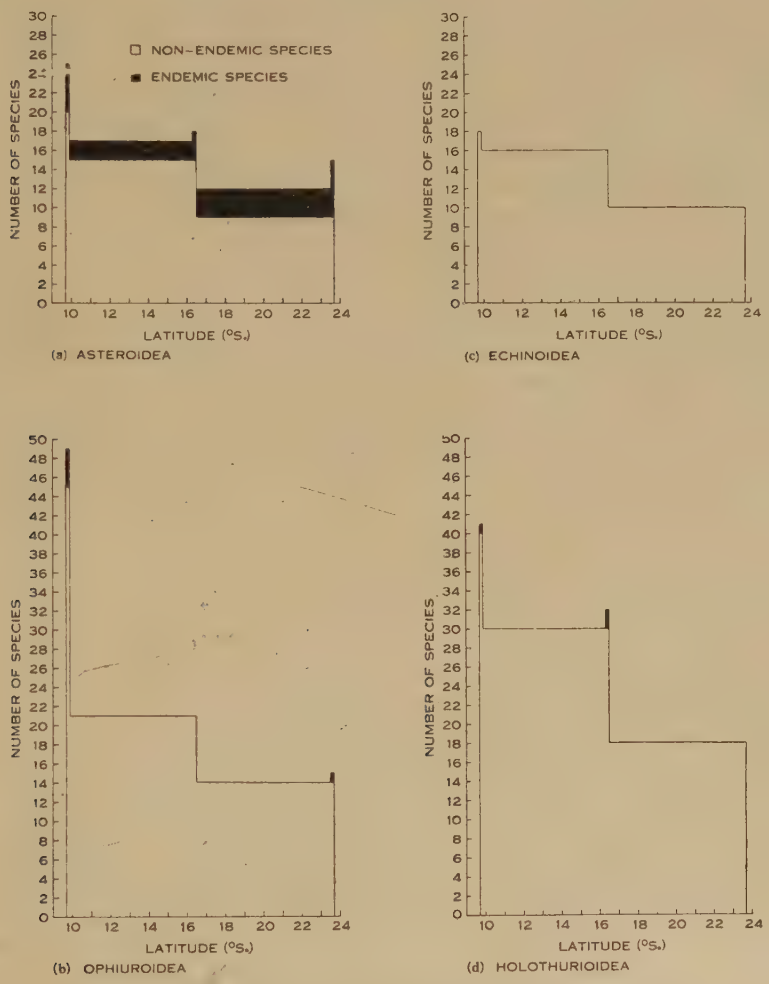

Fig. 4.—Distribution of reef echinoderm species with latitude.

Attenuation with increasing latitude is particularly marked in the ophiuroids (Fig. 4*b*). Of the 49 species of ophiuroids occurring at the Murray Is. (it is assumed that *Ophiomyxa australis* occurs there) only 14 appear to range the length of the Barrier Reef. Seven range south to the vicinity of Low Isles and 18 (4 of which are endemic) have not been recorded south of the Murray Is. *Ophionereis tigris* appears to be endemic to the Capricorn Group.

Eighteen echinoids are believed to occur at the Murray Is. (Fig. 4*c*). (*Prionocidaris verticillata*, *Laganum depressum*, and *Metalia sternalis* are assumed to occur in the Murray Is. region since they occur south of that region, in Barrier Reef waters, and also occur to the north.) Of these 18 species, 2 are not found south of the Murray Is., 6 range as far south as the Low Isles region, and 10 range the length of the Barrier Reef.

Nudechinus multicolor has been recorded in Australian waters only from Low Isles. Elsewhere it has been recorded only from Japan and consequently its range is uncertain.

Although *Echinostrephus molaris* has not been recorded south of Low Isles, an allied species, *E. aciculatus*, occurs at the southern end of the Barrier Reef. It is possible that *E. aciculatus* extends the whole length of the Barrier Reef but has been overlooked by collectors in the northern sector of the Reef. Both *E. aciculatus* and *Nudechinus multicolor* have been omitted from Figure 4*c*.

Thirty-six species of holothurians have been recorded from the Murray Is. (Fig. 4*d*); but as *Holothuria scabra*, *H. paradoxa*, *H. erinaceus*, *H. fusco-olivacea*, and *Chondrocloea recta* have been recorded from coral-dominated localities to the south, and also occur throughout the West Pacific area, it is considered that they occur in the Murray Is. region also. Of the total of 41 species of holothurians believed to occur in this region, 11 have not been recorded to the south, 12 range as far as the Low Isles region, and 18 range the length of the Barrier Reef. *Phyllophorus trapezus* appears to be endemic to Low Isles and *Holothuria axiologa* to the Murray Is., while *Holothuria notabilis* has been recorded only from Low Isles in Barrier Reef waters.

On the whole the attenuation of echinoderm species found on the Great Barrier Reef may be said to be one of constant subtraction from the total number of species found at the northern tip of the Reef, and there are few substitutions.

(*c*) *Species Found on the Queensland Coast South of Lat.* 25° *S.*

There are 12 species found in southern Queensland which have not been recorded north of the biogeographical boundary. Some of these are typical Peronian species (e.g. *Anthenea acuta*, *Phyllacanthus parvispinus*), others range south and west to South Australia (e.g. *Patiriella calcar*, *Petricia vernicina*), and others occur right round the southern half of the continent and north along the west coast of Western Australia to Shark Bay (e.g. *Ophiothrix caespitosa*, *Heliocidaris erythrogramma*). It is of interest that none of the holothurians occurring in south-eastern Australia has extended its range into Queensland waters.

As mentioned earlier, a few tropical echinoderms found commonly at mainland localities range south well into the Peronian Province. Most of these, however, occur only in Moreton Bay. Thus of the 35 species recorded from Moreton Bay, 6 are tropical species which occur as far south as Port Jackson, N.S.W., whilst 24 are tropical species which have not been found elsewhere in the Peronian Province. Of the remainder, 2 probably occur right round Australia, 2 are probably southern species which have extended their ranges to the north of the biogeographical boundary, and 1 is apparently a southern species.

As southern species predominate in oceanic waters encircling Moreton Bay it would appear that a set of ecological factors operates within Moreton Bay which favours tropical species and excludes most southern species. The average summer temperature of the water over the shallow flats is presumably a critical factor (see Endean, Kenny, and Stephenson 1956).

The Moreton Bay population appears to be an isolated one and might be expected to exhibit some degree of incipient speciation. However, this is not the case, presumably because gene interchange with northern echinoderm populations occurs by way of larval stages carried in the Notonectian Current.

This warm current is a branch of the Pacific south equatorial current and impinges on the Queensland coast near Fraser I. It then veers to the south, passing down the New South Wales coast (see Halligan 1921). According to the "Australia Pilot", Volume III (British Admiralty 1950), there are frequently eddies from this current which set northward in inshore waters notably near Moreton Bay.

The occurrence of *Asterina nuda*, *Holothuria atra*, and *H. difficilis* at Caloundra (near the northern entrance to Moreton Bay), but not elsewhere in the Peronian Province, is of interest. These species have been found only in reef waters to the north of the biogeographical boundary. Other species found at Caloundra which are also common on the Barrier Reef are *Holothuria leucospilota*, *H. impatiens*, and *Discucumaria africana*. These three species also have not been found in Moreton Bay. It is possible therefore that tropical species occurring at Caloundra prefer fully saline, fully oxygenated sea-water. Fluctuations in the salinity and oxygen tension of the water must be tolerated by northern echinoderms found in Moreton Bay; and it is of interest that only one (*Chiridota rigida*) of the 29 tropical species found in Moreton Bay is recorded as a reef species.

As the numbers of the northern species found at Caloundra fluctuate considerably from year to year, and in some years some species appear to have been entirely absent, it is possible that they invade the locality periodically when conditions are favourable. Presumably their larval stages are carried to Caloundra by eddies from the warm Notonectian Current which flows south from the Capricorn–Bunker Group region, skirting the eastern Australian coast. Likewise many of the tropical echinoderms found elsewhere in Peronian waters appear to be periodic invaders as was noted by Bennett and Pope (1953).

Thus in Queensland waters south of the biogeographical boundary, both northern and southern species occur but most of the northern species are confined to the Moreton Bay–Caloundra area. A few northern species range well into Peronian waters. However, no southern species (with the possible exceptions of *Nepanthia belcheri* and *Ophiothrix ocestra*, mentioned earlier) has invaded mainland waters north of lat. 25° S., and only one southern species (*Ophidiaster confertus*) occurs also in reef waters.

(*d*) *Species Found at Lord Howe Island*

Of the 48 non-endemic echinoderm species found at Lord Howe I. (lat. 31° 33′ S., long. 159° 5′ E.) 41 have now been recorded from Queensland waters; 36 of these occur in southern Queensland.

It has been postulated that the Notonectian Current was responsible for bringing the larval stages of these species to the island (Endean 1953). In this respect it is significant that most of the common species at Lord Howe I. are common in southern Queensland but are not found on the nearby New South Wales coast. Indeed only two (*Coscinasterias calamaria* (Gray) and *Ophiactis resiliens* Lyman) of these common species are common in New South Wales waters and not yet recorded from southern Queensland.

V. Zoogeographical Affinities of Tropical Australian Echinoderm Fauna

(*a*) *Queensland Fauna*

(i) *Mainland Species.*—A group of 12 species occurring in southern Queensland but not extending their range north of the biogeographical boundary at about lat. 25° S. is omitted from subsequent discussion. These species are Peronian or Peronian and Flindersian with the centres of their distributions to the south. Such species have made a negligible contribution to the fauna north of lat. 25° S.

The range of *Paracaudina australis* is not known with certainty and it too is excluded. Species endemic to the Queensland mainland and species occurring north of lat. 25° S. which are endemic to eastern Australian waters (21 in all), together with 5 species which probably range right around Australia, are also omitted.

The following is an analysis of the occurrence of the 79 remaining species.

Occurrence	Recorded on Australian Coast West of Torres Strait	Not Recorded on Australian Coast West of Torres Strait
Endemic to tropical Australia	21	—
East Indies	25	13
West Pacific	1	1
East Indies and West Pacific	10	8
Total	57	22

It can be seen that the bulk of the 79 species listed have been recorded in Australian waters to the west of Torres Strait. Of the 22 species not recorded west of Torres Strait 21 occur in the East Indies and only 8 of these also occur in the West Pacific Ocean. It is probable therefore that the majority of these 21 species will be found between the Aru Is. and Torres Strait when the echinoderm fauna of that region becomes better known.

Also it will be noted that the bulk of the non-endemic species listed occur in the East Indies. Moreover the nearest relatives of most of the 21 species endemic to tropical Australia (and also of those endemic to Queensland mainland waters) occur commonly in the East Indies (e.g. species belonging to the genera *Astropecten*, *Goniodiscaster*, *Nepanthia*, *Placophiothrix*, *Salmacis*, and *Pentacta*).

Since relatively few of the species listed occur in waters to the east of New Guinea, it would appear that Torres Strait is the principal exchange route used by mainland echinoderms common to Queensland and northern Australia and by those common to Queensland and the East Indies.

It is possible that exchange of mainland species common to Queensland and the East Indies could occur via the northern and eastern shores of New Guinea. However, deep water is found immediately offshore along the northern coast of New Guinea and as both the Mamberamo and Sepik Rivers pour out continually large volumes of fresh water into this area it would seem that there exists a barrier to the spread of littoral echinoderms generally in northern New Guinea waters.

Fig. 5.—Exchange routes used by echinoderm species in tropical Australia. The Tropical Australian Province is stippled.

——▶ Routes used by mainland species.

—·—▶ Routes used by reef species.

Also in south-eastern New Guinea there appears to be a dearth of suitable habitats for mainland echinoderms. Indeed the Papua-Louisiade Barrier Reef and numerous fringing reefs along the south-eastern coastline probably constitute an additional barrier to the movements of mainland species.

On the other hand there is a shallow-water communication between Torres Strait and the East Indies via the west coast of New Guinea and the Aru Is. (see Fig. 5) which could be utilized by the majority of mainland echinoderms.

The spread of Queensland mainland species to the West Pacific area is probably prevented by the fact that Queensland is separated by the deep waters of the Coral Sea from the Solomons, the New Hebrides, and other West Pacific localities. In this connexion it should be noted that echinoderms which are strictly littoral have a limited bathymetrical range and Clark (1921) maintains that they rarely extend into water deeper than 30 fm.

It is possible that species possessing prolonged larval stages could cross deep water as a result of larval transit by currents. However, currents in the Coral Sea area move towards the Queensland coast, not away from it.

(ii) *Reef Species.*—Of the total Queensland echinoderm fauna 94 or 35 per cent. are regarded as reef species, and 15 of these are endemic to eastern Australian waters.

The following is an analysis of the occurrence of the remaining 79 species.

Occurrence	Recorded on Australian Coast West of Torres Strait	Not Recorded on Australian Coast West of Torres Strait
Endemic to tropical Australia	7	—
East Indies	2	12
West Pacific	1	4
East Indies and West Pacific	13	40
Total	23	56

It will be noted that the bulk of the reef species which occur outside Australia do not occur in Australian waters west of Torres Strait. It would seem therefore that exchange of reef species between Queensland waters and the East Indies by way of Torres Strait cannot be of any magnitude, if in fact it occurs at all. The reason for this probably lies in the fact that coral reefs are remarkably sparse in the area immediately west of Torres Strait. Fairbridge (1950, p. 335) says of the Gulf of Carpentaria that "it is rather astonishing to find this enormous shallow water platform averaging 25–30 fathoms almost completely devoid of coral reefs", and (p. 375) that "in the Gulf of Carpentaria . . . much muddy sediment is carried down by the larger rivers of tropical Queensland. This mud and other concomitant factors have largely inhibited coral growth here".

Likewise in southern New Guinea large quantities of fresh water and silt are poured out from coastal rivers such as the Fly River, and coral growth in the region is thereby inhibited. Apparently then there is an ecological barrier to the spread of reef forms to the west of Torres Strait.

Accordingly specific exchange of Queensland and Indo–West Pacific echinoderms must occur chiefly by way of eastern New Guinea and the Coral Sea.

It is doubtful whether adult littoral echinoderms can spread along the northern New Guinea coast as noted earlier. Also there do not appear to be any records of the occurrence of coral structures in this region. Consequently it would seem that reef echinoderms are not well represented in the region if indeed they occur at all. On the other hand reef echinoderms could occur on the Papua-Louisiade Barrier Reef in the waters of south-eastern New Guinea.

Since New Guinea and the Great Barrier Reef are both separated by deep water from localities in the West Pacific area, it would seem that there can be no

exchange of Queensland and Indo–West Pacific species via the Coral Sea route. However, the pelagic young of the West Pacific species could use this route, since in the Coral Sea area a branch of the Pacific south equatorial current, which has passed between the Solomon Is. and the New Hebrides, impinges on the Great Barrier Reef (for seasonal current charts see Endean, Kenny, and Stephenson 1956). It is noteworthy that there can be no movement of Queensland species in the reverse direction, and that gene flow between West Pacific and Queensland populations of various species is unidirectional.

(iii) *Species Occurring in both Reef and Mainland Waters.*—Of the 55 species found both in Barrier Reef and in mainland waters 2 are endemic to tropical Australia, 3 are endemic to Queensland, 1 is a southern form, and 1 occurs right round Australia.

If these are excluded there remain 48 species, 25 of which range to the west of Torres Strait on the Australian coast. Of those ranging to the west of Torres Strait 5 (*Anseropoda rosacea*, *Tamaria megaloplax*, *Ophiarachnella infernalis*, *Temnotrema siamense*, and *Discucumaria africana*) are common East Indian species. Since they have not been recorded from eastern New Guinea or the West Pacific Ocean it is probable that exchange between East Indian and eastern Queensland populations of these species occurs only via Torres Strait.

The remaining 20 species occurring on the Australian mainland west of Torres Strait are found throughout the Indo–Pacific region. Exchange between northern Australian and East Indian populations of these species with Queensland populations no doubt occurs principally via Torres Strait. Gene exchange between West Pacific and Queensland populations probably occurs also as a result of transit of the Coral Sea by larvae.

Of the 23 species not occurring west of Torres Strait in Australian waters, 18 occur in the West Pacific. The principal exchange routes used by West Pacific and Queensland populations of these species would appear to be via the Coral Sea and the east coast of New Guinea. Transport of the pelagic larval stages by currents would again be involved here. The 5 remaining species occur in the East Indies but not in the West Pacific, and will probably be found between Torres Strait and the Aru Is.

(*b*) *Northern Australian Fauna*

If the echinoderm fauna of the region between the Gulf of Carpentaria and Geraldton is examined, using as a principal source of information Clark's (1946) monograph, it will be found that 222 well-authenticated species (belonging to 110 genera) of shallow-water echinoderms (excluding crinoids) occur in this region. Six of these occur right round Australia and are excluded from subsequent discussion.

Of the remaining 216 species, 86 are apparently endemic to the region—particularly to the coastline near Broome—and an additional 30 are endemic to Australia. Of the remainder, 98 occur in the East Indies but only 44 of these occur also in the West Pacific. Two occur elsewhere only in the latter area. Most of the endemic species belong to genera which are common in the East Indies (e.g. *Anthenea*, *Astropecten*, *Goniodiscaster*, *Archaster*, *Protoreaster*, *Nepanthia*, *Macrophiothrix*, *Ophiactis*, *Salmacis*, *Nudechinus*, *Pentacta*, *Thyone*).

It would appear therefore that the echinoderm fauna of tropical Australia west of Torres Strait has stronger affinities with the fauna of the East Indies than with that of any other outside geographical area.

Also, the tropical Australian fauna of the region west of Torres Strait is closely allied to that of Queensland waters. Of the 216 tropical Australian species recorded from the region west of Torres Strait, 107 occur in eastern Queensland waters, comprising 57 mainland species, 23 reef species, and 27 common to both environments. Whilst some of these species do not occur west of Darwin the great majority range west to north-western Australia and many as far as the Shark Bay region on the west coast of Western Australia.

The East Indies are separated from north-western Australia by the Timor Trough, which is over 1000 fm deep (see Fig. 5). This must provide a barrier to the direct exchange of littoral echinoderms between the East Indies and north-western Australia as it has for long in the case of terrestrial animals (Wallace 1869; Mayr 1944*a*). There is the possibility that the pelagic larval stages of some echinoderms could cross this barrier, but in the Timor Trough area the currents move to the west (see Royal Netherlands Meteorological Institute 1949). The only shallow-water communication between Australia and the East Indian region is along the west coast of New Guinea past the Aru Is., and this must be the principal exchange route utilized by mainland species common to the East Indies and tropical Australia. Some echinoderms, either because their bathymetrical range is very restricted or because they are adapted to ecological conditions peculiar to the region they inhabit, appear not able to traverse this shallow-water route. Consequently a number of endemic species occur in northern Australian waters.

There is the further difficulty that several reef species occur in north-western Australia. In this connexion it should be noted that on the coastline of north-western Australia there are regions where rocks and terrigenous sediments predominate and others where corals are commonly found. Fringing reefs are common between Cape Londonderry and Lagrange Bay, between Port Hedland and Onslow, and in the Abrolhos further to the west (Fairbridge 1950). It is in such regions that reef species occur.

It has already been noted that there is a dearth of coral structures immediately to the west of Torres Strait and that it is unlikely that reef species can pass in either direction through this region.

Of possible significance with respect to the exchange of reef species between the waters of north-western Australia and those of the East Indies is the occurrence of a series of reef platforms and atolls along the margins of the Sahul Shelf and the Rowley Shelf (Teichert and Fairbridge 1948; Fairbridge 1950). Also near-shore reef platforms are of common occurrence in the region. These atolls and reef platforms could provide stepping stones for exchange of reef species found in the East Indies and north-western Australia.

It is significant in view of the above that only one reef species common to Queensland and north-western Australia has not been recorded from the East Indies.

VI. The Apparent Origin of the Fauna of Tropical Australia

There is evidence that during the Palaeozoic and Mesozoic Eras the Australian continent extended much further north and east than it does to-day. Abendanon (1919) postulated a Palaeozoic continent stretching from Tasmania to the Celebes, and Fairbridge (1953) has summarized palaeogeographic and zoogeographic data which indicate that much of northern Australia and its continental shelf "formerly extended far to the north-west, including the northern Molluccas, in Mesozoic times and possibly reaching to the Celebes in the late Palaeozoic" (p. 29).

During the Mesozoic too, the available evidence suggests that the Australian continent extended out into the Pacific Ocean well beyond its present limits—possibly as far as the Marshall Line (see Fig. 5)—although there were apparently occasional transgressions by the sea during this and the preceding era (see Benson 1923, 1924; Bryan 1944).

Fairbridge (1953) noted that during the Permian and Triassic periods the geosynclinal evolution of the Timor-Banda arc caused the sea to encroach on the old continent. Benson (1923, 1924) postulated that this geosyncline extended during the Trias around New Guinea to New Caledonia and New Zealand, thereby disrupting the old continent.

Mayr (1944*a*), on zoogeographical grounds, followed Kuenen (1935) in believing that there were continental connexions between the East Indies and Australia until the early Eocene, but that from the Eocene to the early Pleistocene there was complete separation of these two regions. Thus by the beginning of the Tertiary the relation of the Australian land-mass to the seas around it was probably much as at present, and Indo-Pacific echinoderms were given the opportunity to invade what appears to have been a virgin region in northern and north-eastern Australia.

Clark (1921) postulated that when, as a result of the depression of land areas to the east of New Guinea, what is now the Coral Sea became linked with the Pacific Ocean (see Hedley 1909) an influx into Queensland waters of Pacific echinoderms already present on the north-eastern shores of the old continent occurred. This influx he believed gave rise to a major part of the Queensland fauna, "not only of the Murray Is. and Barrier Reef, but of the coast of tropical Queensland as well" (Clark 1921, p. 209).

Clark also maintained that when the Indian Ocean and the Coral Sea became united by the formation of Torres Strait, a migration of East Indian echinoderms present in northern Australian waters occurred. Many of the migrating species passed eastward and southward "to mingle on the Queensland coast with the species of the Pacific Influx" (Clark 1921, p. 212). Thus according to Clark the present-day echinoderm fauna of the eastern Australian coast is a result of the mixing of the Pacific influx with the Torres Strait migrants. Of these two introductions he believed that the former was the more important.

Unfortunately there is a lack of Tertiary sediments from Queensland waters, as would be expected, and palaeontology can therefore throw no light on early migrations to this region. Apparently, however, many of the invading echinoderms extended their ranges to south-eastern Australia. Barraclough Fell (1953, p. 254)

noted that the "Australian and New Zealand Tertiary echinoderm faunas show marked similarities throughout those portions of the stratigraphical record represented by comparable deposits on either side of the Tasman Sea", and that these faunas had a common origin in the Indo-Pacific.

Clark (1921) believed that the early echinoderm migrants were the ancestors of the present echinoderm fauna of the Queensland coast. However, these early species could not have been the immediate ancestors of the present ones. Despite the paucity of endemic genera in this region today, such genera originated in mid-Tertiary times in or near Australasia, and there is evidence that a northward migration occurred as pointed out by Barraclough Fell (1953). This author also noted that in the late Miocene a great extinction of the old echinoderm fauna occurred. Other marine groups suffered a similar fate (Fleming 1949). Both authors attribute this occurrence to a cooling climate. Subsequently in the Pliocene, a new Indo-Pacific stock entered eastern Australian waters.

Thus the available evidence indicates that the present Queensland echinoderm fauna is derived from a recent Indo-Pacific stock.

As noted earlier, zoogeographical evidence indicates that from the Eocene to the Pleistocene there were no land barriers to the migration of marine organisms round tropical Australia. This poses two problems:

(*a*) Since no barriers were present, there would be little likelihood of populations becoming isolated for a sufficient length of time for mutations to accumulate and so give rise to the region's present-day endemic species.

(*b*) There are over twice as many endemic species in the tropical waters of Australia west of Torres Strait as in eastern Queensland waters, and yet northern Australian waters are in direct contact with an outside geographical area and have been, apparently, since the Eocene. Clark (1921) accounts for the large number of endemic forms in north-western Australian waters by postulating (p. 209) that whilst "New Guinea and Australia were still united as one land mass, a bay of the Indian Ocean lay to the north-west of what is now Torres Strait", and that "the echinoderms occupying the southeastern shores of this bay or sea formed the first echinoderm fauna of Australia". This fauna, Clark believed, still forms a large part of the fauna of northern Australia west of Torres Strait.

However, if, as zoogeographical and geological evidence indicates, Australia was separated from the East Indian region as early as the Eocene period then it is apparent that these early species could not have been the immediate ancestors of the region's present-day species. As mentioned earlier, a number of genera have appeared in the Australasian region since the Eocene, many of these having reached Australia via the East Indian region, and some having originated in Australasia and migrated northwards. Moreover there is the question of the age of species to be considered. Ekman (1953) postulates that the average age of species belonging to the crinoids, decapod crustaceans, and sea urchins is at most 4 to 6 million years. He also notes (p. 29) that a period of a million years was "sufficient for a fairly large number of animal species to undergo changes of a magnitude which differentiated them as new species".

Accordingly it is necessary to examine the recent (Quaternary) history of tropical Australia if light is to be thrown on the present-day specific composition of the echinoderms in the area. A study of probable conditions in the area during the Pleistocene ice ages is especially useful.

During the Pleistocene, eustatic lowerings of sea-level occurred with a minimum fall of 50 fm (Daly 1934; Zeuner 1945; Fairbridge 1950). This was more than sufficient to link New Guinea to Australia. (Fairbridge (1953) states that an emergence of less than 10 fm would provide a bridge from New Guinea to Australia.) Thus a major biogeographical barrier to the dispersal of echinoderms around tropical Australia was set up. Moreover it is probable that the climate on the two sides of this barrier differed. Thus Mayr (1944*b*) and Gentilli (1949) state that possibly north-western Australia had an arid climate during this period, whilst Stanley (1928) maintained that it was only in the warmer northern half (north of lat. 17° S.) of the present Barrier Reef area that coral reefs could be expected during the Pleistocene.

The closure of Torres Strait would separate echinoderm stocks on either side. Populations of mainland species on opposite sides of this barrier could then diverge genetically, provided of course there was no direct contact between these populations via northern New Guinea. There is no evidence that such contact existed. On the contrary it is likely that barriers to the movement of marine species round north-western New Guinea were set up in the East Indies during the Pleistocene falls in sea-level.

It would be expected that, if the above hypothesis is substantially correct, mainland species would evolve east of Torres Strait which would have marked affinities with the East Indian or northern Australian species from which they were derived.

Of the Sahul Shelf area of north-western Australia Fairbridge (1953) remarks that "for long periods during the Pleistocene, the great transverse 'rises' recognised in the regional bathymetry of the Sahul Shelf would have been emergent promontories . . . Most of the depressions on the other hand with their broad shallow bays would seem to favour the development of extensive mangrove swamps, whilst the Bonaparte depression may have been reduced to a swampy lake whenever the sea-level was more than 30-40 fathoms below the present".

Thus in the Sahul Shelf area numerous echinoderm populations could have been isolated—a prerequisite for speciation—and possibly this accounts in large measure for the numerous endemic species found there today.

Subsequently, with the final retreat of the Pleistocene ice caps and the final rise in sea-level that attended this, Torres Strait was reopened, barriers to migration around northern and north-western Australia and probably in the East Indian area to the north were broken down. Echinoderms could once more spread around tropical Australia, extending their ranges southwards as the climate warmed. Some appear to have done so but others seem restricted to short regions of the coastline.

Many species originating in East Indian waters during the Pleistocene could then extend their ranges into Australian waters, and vice versa. Others, possibly because they were adapted to specialized habitats or because their bathymetrical ranges

were restricted, did not spread between the two geographical areas; or, if they did spread initially, populations in the two areas were isolated subsequently by the deepening waters of the post-glacial period. Amongst these would be found many of the species endemic to tropical Australian waters.

Thus in tropical Australia today there should be closely allied species some of which are sympatric (because subsequent to the breakdown of isolating barriers their ranges have overlapped) and others allopatric.

Sympatric Species

Astropecten monacanthus, *A. granulatus*, *A. pulcherrimus* Clark
Stellaster incei, *S. princeps*
Anthenea australiae Doderlein, *A. conjungens* Doderlein
Pentaceraster gracilis, *P. australis*
Tamaria megaloplax, *T. tumescens* (Koehler)
Nepanthia variabilis Clark, *N. tenuis* Clark
Nepanthia brevis, *N. belcheri*
Amphioplus depressus, *A. didymus* Clark, *A. stenaspis* Clark
Ophionephthys octacantha, *O. decacantha* Clark, *O. tenuis* Clark
Amphiura microsoma, *A. stictacantha* Clark, *A. phrixa* Clark, *A. velox* Koehler, *A. bidentata*
Ophiarachnella gorgonia, *O. rugosa* Clark
Ophiotrichoides martensi australis, *O. smaragdina* (Studer)
Ophiactis modesta, *O. fuscolineata* Clark
Salmacis sphaeroides, *S. belli*
Nudechinus darnleyensis, *N. scotiopremnus* Clark
Actinocucumis typicus, *A. difficilis*, *A. longipedes* Clark
Thyone papuensis, *T. micra* Clark, *T. buccalis*, *T. minuta* Clark
Phyllophorus trapezus, *P. parvipedes* Clark

Allopatric Species

Archaster typicus, *A. laevis* Clark
Goniodiscaster pleyadella, *G. integer*
Anthenea mertoni, *A. acanthoides*
Protoreaster nodosus, *P. nodulosus* (Perrier)
Echinaster luzonicus, *E. superbus* Clark
Phyllacanthus imperialis, *P. irregularis* Mortensen
Temnotrema bothryoides, *T. elegans* Mortensen

It may be found that the few characters which distinguish *Goniodiscaster pleyadella* and *G. integer* form parallel clines, and *G. integer* may be merely a variant of *G. pleyadella* which inhabits slightly cooler waters. However, the pairs of allopatric species listed seem generally to inhabit comparable environments. This is also true of most of the pairs or groups of sympatric species mentioned, and it seems a reasonable conclusion that many of them have arisen from geographical isolates which initially diverged genetically during the Pleistocene lowerings of sea-level.

It would be expected that during the Pleistocene ice ages reef species would retreat northwards. Because of the great depth of water between the Barrier Reef and the West Pacific area it is unlikely that populations of species at present common to both areas would have been isolated. As the climate warmed in the post-glacial era reefs would appear in the southern half of the Great Barrier Reef area and gradually reef echinoderms could have extended their ranges southwards.

VII. Limits of Tropical Marine Provinces

It has been shown that the Queensland mainland and Barrier Reef echinoderm faunas are in the main distinct entities, and that the mainland fauna has strong affinities with that of the East Indies whilst the Barrier Reef fauna has strong ties with that of the West Pacific area.

It would seem logical therefore to follow Whitley (1932) in restricting the Solanderian Province to the Great Barrier Reef area. However, Whitley's proposal that the area inhabited by the fauna of the Queensland mainland inside reef waters north of the Peronian Province be regarded as a separate province, the "Banksian", requires modification. Firstly, the echinoderm fauna of the continental islands must be grouped with the mainland fauna proper (see also Endean, Stephenson, and Kenny 1956). Secondly, it is extremely doubtful whether Torres Strait can be regarded as a natural geographical barrier preventing "Banksian" echinoderms from ranging into the Dampierian Province and vice versa.

Of the 118 mainland echinoderm species found in Queensland waters 12 do not occur north of lat. 25° S. If these be excluded, together with 21 species which are endemic either to Torres Strait or to regions of the coast south of that locality, 1 species (*Paracaudina australis*) whose range is uncertain, and 2 species not found east of the Gulf of Carpentaria, there remain 82 species.

Of these 11 have not been recorded south of Torres Strait but range to the west of that locality on the northern Australian coast or are considered to occur between the East Indies and Torres Strait. Another 7 species range south of Torres Strait in Queensland mainland waters but have not been recorded to the west of Torres Strait in northern Australian waters and possibly do not occur between that locality and the East Indies.

However, to 64 of the 82 species considered, Torres Strait does not seem to present a barrier to migration in either direction. Moreover, echinoderms have not been as intensively collected between Direction I. and Torres Strait, nor in the Gulf of Carpentaria, as in the Torres Strait region. It is probable that some of the echinoderms to which Torres Strait appears to be a barrier have actually extended their ranges through this region.

Thus to Queensland mainland echinoderms generally Torres Strait does not present a major biogeographical barrier. Indeed, there is no evidence that any natural biogeographical boundary exists between Hedley's Dampierian Province and Whitley's Banksian Province. This apparent lack of any major barrier between the faunas of the two provinces indicates that they may be considered a single faunistic unit. Neither Hedley (1904, 1926) nor Clark (1946) separated the Barrier Reef fauna from the Queensland mainland fauna. Very few Barrier Reef species have extended their range through Torres Strait, and presumably this is the basic reason why these authors placed the boundary between the Dampierian and Solanderian Provinces at Torres Strait.

On the other hand, one of the basic requirements for the fauna of a geographical area to be classed as an entity distinct from those of adjoining areas is that it should possess endemic forms. The more endemic species it possesses the more distinct it

is from other areas. A high degree of endemism characterizes the echinoderm fauna of north-western Australia, but it remains to be seen whether this is more apparent than real. A number of species previously thought to be endemic to north-western Australia have been found in Queensland in recent years.

Another mode of delimiting faunistic provinces is based on changes in the degree of dominance exhibited by members of a group of species found along a strip of coast. Stephenson (1948, p. 213) remarks that in some cases "the mixture is so obvious and covers such a long strip of coast that the area which it occupies is recognizably distinct from neighbouring areas, even if it has few or any endemic forms". In such cases the fauna of adjacent faunistic provinces would overlap considerably and the line of demarcation between these provinces would not be sharply defined.

For many of the echinoderms and other marine invertebrates of northern Australia, the full extent of individual ranges of species and the degree of dominance possessed by each species are not known.

It is possible that, if the recent histories of the marine fauna of north-western Australia and that of Queensland have differed, as postulated in Section VI, a line of demarcation between the Dampierian and Banksian Provinces can be drawn in the waters of northern Australia. The apparent high degree of endemism exhibited by echinoderms in north-western Australia strengthens this possibility. However, the question of existence of a faunistic boundary in northern Australian waters awaits resolution by future research. For the present the known distribution of Australia's tropical echinoderms (excluding those belonging to the Solanderian fauna) indicates that they belong to a single Tropical Australian Province.

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A NEW CLASSIFICATION OF THE AUSTRALIAN MARGINELLIDAE (MOLLUSCA), WITH A REVIEW OF SPECIES FROM THE SOLANDERIAN AND DAMPIERIAN ZOOGEOGRAPHICAL PROVINCES

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Summary

A new classification is proposed for the Australian Marginellidae, both Recent and Tertiary. Most previous papers and all Australian papers have previously referred to the many species under one genus *Marginella*, though occasionally they have been subdivided into several sections without generic names. This subdivision has now been carried farther, and the approximately 200 Australian species have been divided into 33 genera, of which 31 are new and 2 have been recently named from Japan. Of the 33 genera 22 are Recent and 20 Tertiary, and 9 Recent and Tertiary genera are considered congeneric. Figures are shown of all the type species, and a key is provided to those still living in Australian seas.

The second part of the paper reviews and figures all the known species from the Solanderian and Dampierian Zoogeographical Provinces. Species number 41, of which 33 are proposed as new. Of these, 37 are Solanderian and 9 Dampierian. Five species are common to the Solanderian and Dampierian and one to the Solanderian and Peronian, and one ranges through the Maugean, Flindersian, Peronian, Solanderian, and Dampierian Provinces.

A. THE CLASSIFICATION OF AUSTRALIAN MARGINELLIDAE

Discussion

The problem whether *Marginella* should be retained as a single genus to cover a great number of species from all of the seas of the world, or whether it should be divided into a number of genera or subgenera, has always been controversial. The genus was proposed by Lamarck as long ago as 1799. The shell characters were distinctive and easily definable, and for many years the genus was quite sufficient to cover the comparatively few species then known. As more and more species were discovered, however, the genus became cumbersome, and various attempts were made to subdivide it into convenient groups. A limited number of new names were proposed, mainly for some of the larger and highly coloured tropical species—particularly those from West Africa, which were the best known. During the latter half of the nineteenth and in the early twentieth century, before the problems of geographical distribution and the constitution of zoogeographical provinces were considered of importance, the group was monographed a number of times, always as a world entity. Among these monographs may be cited those of Sowerby (1847) and Tryon (1883). In these *Marginella* was retained in the broadest sense, but a few other names were used as subgenera in brackets, and the whole group was divided into a number of sections. The latest comprehensive work was by Tomlin (1917), who reviewed the literature and listed the known species, both recent and fossil. Tomlin held that any one character selected for generic subdivision cut indiscrimin-

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ately across all other characters, and beyond the use of unnamed sections was content to retain *Marginella* in the widest sense.

In recent years Habe (1951) has reviewed 12 Japanese species, dividing them into 5 genera, 3 of which he proposed as new. Of these genera 2 are now considered congeneric with Australian forms and have been used in the present classification.

In Australia *Marginella* alone has invariably been used. Hedley (1917), May (1921, 1923), Cotton (1944, 1949), and Laseron (1948) either listed or monographed the group from the temperate Australian provinces. Cotton alone divided it into sections, remarking (1949, p. 198): "It is doubtful whether any of the named 'genera' other than *Marginella* used in the wide sense are represented in Australia. *Marginella* itself has a dozen 'subgenera', and it would be difficult and probably inaccurate to even allot Australian species to any of these subgenera". The author (1948) held much the same views when he monographed the Peronian species. The present review of the Australian tropical species, however, about which very little was previously known, makes it possible for the first time to survey the family in Australia as a whole. Australia has the greatest known concentration of Marginellidae in the world, about 200 species in all, and it is considered that sufficient is now known to enable the whole problem to be reconsidered.

The problem of *Marginella* is curiously akin to that of *Cypraea*, with slight and to a certain extent psychological differences. If the marginellas were as large and handsome as the cowries and had the same universal appeal to collectors and conchologists, they would surely have already been split into different genera to the same extent. Yet the number of species is at least twice and probably three times as great as in *Cypraea*. The shell also is more variable in form and there are more definable differences on which to base a subdivision. The main difficulty is that shell characters, while constant in each species, are variously mixed in each group, and it is impossible to select one or two to form primary subdivisions. It is nevertheless possible to recognize numerous small groups of obviously related species, and to note a number of characters common to each group. There seems no half-way measure. Either *Marginella* must be retained as a whole, or it must be split into a large number of genera, each of which covers a relatively small number of species It is felt there can be no logical objection to this, provided that the characters are readily recognizable and that the proposed new genera are clearly defined.

From the world point of view one major subdivision can be broadly detected, though on shell characters alone it is ill defined. There does seem to be a difference between the Pacific, particularly the temperate Pacific, species and those from the Atlantic and West Indian Oceans. This applies to the Tertiary species as well as to those still living. It is noteworthy that the Australian Tertiary, mainly Miocene, is richer in Marginellidae than any other Tertiary fauna, and also that the Australian recent species of the family probably outnumber those from all other areas put together. It would seem that the early Australian Tertiary is the possible source of their distribution and evolution. In addition the Australian Tertiary species bear on the whole a distinct resemblance to those still living in the local seas, and of the genera here proposed nine are considered to have survived throughout this vast lapse of time.

Outside Australia the family is largely concentrated both in number of species and individuals, in limited areas. Of these areas West Africa is the most noteworthy. There is another concentration on the East African coast; a number occur in the Indian Ocean and also in the East Indies, 12 species in Japan, and 25 species have been described from New Zealand. Elsewhere they are either altogether absent or at most are represented by one or two species.

A few species occur in the European Tertiary, and these were reviewed by Cossman (1899). In the same paper he also reviewed the few Australian fossil species which had already been described by Tate. Cossman used a few genera apart from *Marginella*; for instance, he referred *cassidiformis* Tate to the Eocene *Faba* of Fischer. For this species the new genus *Urniginella* is now proposed. Of the other genera used by Cossman *Stazzania* Sacco, the type of which is Miocene, is not unlike *Austroginella*, while the Eocene *Dentimargo* Cossman somewhat resembles the Australian Miocene *Stromboginella*. At this stage of our knowledge, however, it is felt that any attempt to correlate Australian with European Tertiary forms by using the same generic names conveys a sense of relationship which may have little foundation in fact.

Compared with Pacific living species Atlantic species are almost invariably larger, many being upwards of an inch in length, and are generally gaily coloured, either uniformly or with spots and stripes. The texture also is slightly different. Australian species are nearly all small, often minute, rarely over 5 or 6 mm; most are pure white, highly polished, with a porcellanous texture. Very few are coloured, and in these the colouring is confined to a few transverse bands.

Australia is very rich in species, each of the zoogeographical provinces having about 40, that is, about 200 in all, with about 40 so far known from the southern Tertiary. The complete stratigraphy of the Tertiary beds has not yet been satisfactorily settled, but they probably range from the Oligocene to the Pliocene, and have mostly been referred to the Miocene. Even more important than the number of living species is the number of individuals. In the temperate waters of southern Australia they are mostly inhabitants of the sand below low water on the outer beaches, but they also range downwards over most of the continental shelf. Where the location is suitable they exist in enormous numbers, and their shells may form a high proportion of the debris thrown up by the tides. Yet except in dredgings they are seldom seen alive. From their numbers alone it is obvious that they must play an important part in the marine ecology of southern Australia. In northern Australia the variety of species remains about the same but the number of individuals dwindles, and on the beaches they are relatively rare, forming only a minute proportion of the total molluscan fauna. In deeper water, judging from the few dredgings, they are fairly common on sandy bottoms, but again numerically they are of small importance compared with the south.

Prior to this paper very little work had been done on the northern species. Only 5 species (excluding *Marginella valida* Watson) had been described from Queensland, and 5 other species rightly or wrongly recorded from that State. Of the latter 3 are now rejected. Some Peronian species do occur in southern Queensland

below the Tropic of Capricorn, but as this area is now considered part of the Peronian Province they are not listed here. Only 2 species were previously known from the Dampierian Province, and these are from north-western Australia. The list of these is probably still far from complete. But as the greatest variety in any one locality occurs in Torres Strait, and as this is the meeting place of the Dampierian and Solanderian faunas, it is probable that some of these species are truly Dampierian species which have spread to the east. In all, the number of species is now increased to 41, of which 37 are Solanderian and 9 Dampierian, 4 are common to the two provinces, and 1, *Ovaginella ovulum* Sowerby, is common to the Maugean, Peronian, and Solanderian; while *Euliginella angasi* (Crosse) has practically an Australia-wide range, and is found in the Maugean, Flindersian, Peronian, Solanderian, and Dampierian Provinces.

In addition to the 41 species here recognized and figured, 2 other species are considered either doubtful or awaiting confirmation. *Marginella valida* Watson from Torres Strait was considered by Hedley a synonym of *Protoginella lavigata* (Brazier), and reference to the figure and description suggest that the type might well be an immature specimen of that species (see Watson (1886, Plate 16, Fig. 3)). *Marginella australis* Hinds (1844, p. 75) was described as from coral sand at low water on the north-west coast of Australia, the type being in the Cuming Collection. It is depicted as a medium-sized, handsome species, which is referable to the new genus *Sinuginella*, but it has not since been recognized, and lack of material precludes any description or figure.

It is believed that the material forming the basis of this research is practically all that is available. Though a vast amount of collecting has been done on the Queensland coast and the Barrier Reef, few collectors have bothered to seek any of the small shells at all. Much is owed to the few enthusiasts who were either on the staff of or associated in an honorary capacity with the Australian Museum. Of these Mr. John Brazier, Mr. Charles Hedley, and Mr. Alan McCulloch were outstanding. All collected extensively in Queensland, and neglected nothing, however small. In later years Mr. Tom Iredale collected extensively at Michaelmas Cay and Lindeman I., and the author's son John Laseron at Heron I., Bowen, and Gladstone. He too has provided much of the only Dampierian material from Darwin, supplemented by dredgings made by Mr. Mel. Ward in the same area. Inquiries from other sources have so far produced nothing at all.

Specific determination is relatively easy. Most of the species are remarkably constant in shell characters, and when some variation occurs it is generally confined within narrow limits. This probably means that most of the species are of some antiquity and have become fixed with time. Most have a considerable range, generally but not always within one zoogeographical province, and there is little tendency towards the development of local geographical races. Even in the one or two variable species, the variation occurs among individuals from the same locality, and can be paralleled by the same variation between individuals from elsewhere. This is particularly noticeable in *Euliginella angasi* (Crosse), and has led to this species being described at various times under several different names. This species also has the widest range of any noted, the range being practically Australia-wide.

Of the characters used in generic determination none is sufficiently outstanding to be of use in a primary subdivision, each character at times being combined with any of the others. Amongst these characters the length of the spire can be very distinctive, and there is a great difference in facies between such species as are entirely involute and those which have an elevated spire of several whorls. Cotton (1949) indeed makes this the basis of the seven sections he uses. A great variety of contour is also produced by the shoulder of the aperture, produced where the outer lip posteriorly meets the previous whorl. This may be arched, sometimes above the summit; it may be sloping and almost in the line of the spire, or even alate. It may also be deeply sinuate within. A character which may have anatomical significance is the presence or absence of an anterior sinus. Either the anterior margin is rounded or the sinus is distinct and semicircular. This character is easily recognized and is considered of distinct generic importance. The outer lip may be smooth within or denticulate, sometimes strongly so, and this again has been used in generic determination. Plications of the inner margin are also important. In some genera they are strong and transverse, occupying more than half the aperture; in others they are thin and oblique and anteriorly placed. They are generally four in number, but occasionally less, or may be multiplicate. The number of plications is not always easy to determine, and in some species the posterior plications are right within the shell, and are only visible when portion of the shell is broken away (see Fig. 44). This necessitates caution in identifying species which have been described as having only from one to three plications, as some of these have proved to be multiplicate when the interior has been examined.

From these characters all the Australian species are now divided into 33 genera. *Marginella, sensu stricto*, does not occur in Australia at all. Of the genera proposed 22 are living, and 20 have been found in the Tertiary strata of Victoria and South Australia. Of these 9 living are considered as congeneric with fossil genera, and in the others there is such a general resemblance that close relationship is suggested. It is considered that here is further evidence that the present Australian marine fauna, particularly that of the southern temperate provinces, is a direct derivative of that of the local Tertiary.

The following is a key to the Australian Recent genera now described, and to supplement it Figures 1–22 show all the type species, and Figures 23–33 all the type species of genera which so far are exclusively fossil, and presumably extinct.

Key to Recent Australian Genera of Marginellidae

1.	Spire completely involute, not visible	2
	Spire just visible, depressed	4
	Spire elevated, short to medium	6
	Spire elevated, long	13
2(1).	With anterior sinus	*Epiginella*, gen. nov.
	Without anterior sinus	3
3(2).	Elongate, outer margin smooth	*Ovaginella*, gen. nov.
	Short and round, outer margin denticulate	*Microginella*, gen. nov.
4(1).	With anterior sinus	*Phyloginella*, gen. nov.
	Without anterior sinus	5

5(4). Plications 4 or less ..... *Triginella*, gen. nov.
Multiplicate ..... *Euliginella*, gen. nov.

6(1). With anterior sinus 7
Without anterior sinus 9

7(6). Whorls axially plicate ..... *Mesoginella*, gen. nov.
Whorls smooth 8

8(7). Outer margin smooth ..... *Sinuginella*, gen. nov.
Outer margin dentate ..... *Kogomea* Habe

9(6). Whorls axially plicate ..... *Spiroginella*, gen. nov.
Whorls smooth 10

10(9). Form ovate to subovate 11
Form cylindrical to subcylindrical 12

11(10). Plications weak, at anterior end ..... *Neptoginella*, gen. nov.
Plications strong, transverse, occupying more than half the aperture ..... *Deviginella*, gen. nov.

12(10). Outer margin smooth ..... *Haloginella*, gen. nov.
Outer margin dentate ..... *Hydroginella*, gen. nov.

13(1). Strombiform, shoulder of aperture alate 14
Biconical, shoulder of aperture sloping 18

14(13). With anterior sinus 15
Without anterior sinus 16

15(14). Axially plicate on whorls ..... *Plicaginella*, gen. nov.
Whorls smooth ..... *Austroginella*, gen. nov.

16(14). Outer margin denticulate 17
Outer margin smooth ..... *Alaginella*, gen. nov.

17(16). Whorls rounded ..... *Protoginella*, gen. nov.
Whorls carinate ..... *Carinaginella*, gen. nov.

18(13). Plications strong, more than half the aperture 19
Plications weak, anteriorly placed ..... *Baroginella*, gen. nov.

19(18). Outer margin smooth ..... *Longinella*, gen. nov.
Outer margin denticulate ..... *Volvarinella* Habe

Description of Australian Recent Genera

Genus EPIGINELLA, gen. nov.

Type species *Epiginella ablita*, sp. nov. (Fig. 1).

Shell small, form broadly oval, domed above, spire completely involute, smooth and polished. Aperture with a regular rounded outer margin, thickened but without an appreciable varix, smooth and not dentate within, anterior sinus strong and deep, inner margin multiplicate.

From most recent forms with involute spires *Epiginella* can be readily separated by the strong anterior sinus. The fossil *Vetaginella* is close but has a strongly dentate outer lip. The Western Australian species *newmanae* Cotton may be placed in *Epiginella* as it is multiplicate, but it also resembles *Vetaginella* in having a dentate outer lip. *M. concamerata* May will also come here.

Genus OVAGINELLA, gen. nov.

Type species *Marginella ovulum* Sowerby (Fig. 2).

Shell generally of moderate size, but it may be minute, oval, elongate, white, spire completely involute, smooth and polished. Aperture long, arched posteriorly above the summit, outer margin with a heavy, continuous varix, smooth within, rounded anteriorly without a sinus. Inner margin with 3 or 4 plications, close together, anteriorly placed, the anterior 2 generally strong, the others weak.

This is a well-defined group, separable from *Epiginella* by the absence of an anterior sinus, and from *Microginella* which is more rotund, is multiplicate, and has a dentate outer lip. Amongst other species *whani* Pritchard & Gatliff, *nielseni* Laseron, and *cylichnella* May come here.

Genus MICROGINELLA, gen. nov.

Type species *Marginella anxia* Hedley (Fig. 3).

Generally minute in size, rotund, spire completely involute, white or yellow, smooth and polished. Aperture with a rounded outer margin, commencing on the summit of the shell, varix not heavy, but the margin infolded and thickened, outer lip finely dentate within, rounded anteriorly and without a sinus. Inner margin generally multiplicate, the 2 anterior plications strong and oblique, those above generally weak, often quite within the aperture and invisible from in front.

This seems a natural group, and quite a number of species come here, amongst them the well-known Peronian *nympha* Brazier, and the southern species *tomliniana* May, *multidentata* May, *petterdi* Beddome, and *erma* Cotton. Among fossil species *septemplicata* Tate and *moana* Ludbrook are referable to *Microginella*. The fossil species are larger than those still living.

Genus PHYLOGINELLA, gen. nov.

Type species *Phyloginella compressa*, sp. nov. (Fig. 4).

Form ovate or subovate, widest at the shoulder, nearly involute, the spire depressed and just visible from in front. Aperture long, with a rounded shoulder, outer margin smooth within, anterior sinus strong. Inner margin with 3 or 4 plications, weak and anteriorly placed.

This is the first of several genera with short depressed spires. It differs from all these by the anterior sinus. It more closely resembles *Sinuginella*, which has a similar sinus but a more elevated spire, stronger plications, and quite a different facies. Most of the species are tropical while *Sinuginella* has a temperate range.

Genus TRIGINELLA, gen. nov.

Type species *Marginella malina* Hedley (Fig. 5).

The so far unique type is a minute shell, from the continental shelf in New South Wales, which will not fit with any of the other genera proposed but is nearest to *Euliginella*. From this it differs by the peculiar subtrigonal form, being very wide above with a nearly flat summit, tapering and restricted at the anterior end. The

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Figs. 1–22.—Type species of Recent genera of Australian Marginellidae. Fig. 1.—*Epiginella ablita*, sp. nov. Fig. 2.—*Ovaginella ovulum* (Sowerby). Fig. 3.—*Microginella anxia* (Hedley). Fig. 4.—*Phyloginella compressa*, sp. nov. Fig. 5.—*Triginella matina* (Hedley). Fig. 6.—*Euliginella angasi* (Crosse). Fig. 7.—*Mesoginella turbinata* (Sowerby). Fig. 8.—*Sinuginella inconspicua* (Sowerby). Fig. 9.—*Kogomea novemprovincialis* (Yokoyama). Fig. 10.—*Spiroginella leia* (Cotton). Fig. 11.—*Neptoginella fascicula*, sp. nov. Fig. 12.—*Deviginella brachia* (Watson). Fig. 13.—*Haloginella mustelina* (Angas). Fig. 14.—*Hydroginella dispersa*, sp. nov. Fig. 15.—*Plicaginella formicula* (Lamarck). Fig. 16.—*Austroginella muscaria* (Lamarck). Fig. 17.—*Protoginella lavigata* (Brazier). Fig. 18.—*Carinaginella carinata* (Smith). Fig. 19.—*Alaginella ochracea* (Angas). Fig. 20.—*Longinella maugeana* (Hedley). Fig. 21.—*Volvarinella makiyami* Habe. Fig. 22.—*Baroginella infirma*, sp. nov.

aperture is arched above the summit and rounded at the anterior end; the inner margin has 4 plications which are weak and oblique.

Genus EULIGINELLA, gen. nov.

Type species *Marginella angasi* Crosse (Fig. 6).

Euliginella is proposed for a group of nearly always minute, ovate, white shells, with low, depressed, and barely visible spires, the aperture with rounded shoulders often arched above the summit, rounded and without a sinus anteriorly, the inner margin generally multiplicate.

A number of species come within this description, including *multidentata* May and *subauriculata* May. These may be considered typical, but other species have been described as having less than 4 plications on the inner margin. Among these *freycineti* May and *lubrica* Petterd may be mentioned. This character, however, needs particular care in determination, as it often happens that only the anterior plications are visible from in front, and the others are hidden right within the aperture. The minute size of the shell makes this hard to detect. The fossil *rotunda* seems a typical *Euliginella*.

Genus MESOGINELLA, gen. nov.

Type species *Marginella turbinata* Sowerby (Fig. 7).

Shell subconical, broad at the shoulder, with a relatively slight anterior taper, spire short but slightly elevated, whorls with axial plications on the shoulder, but these may be nearly obsolete. Aperture shouldered posteriorly, outer margin with a strong varix, smooth within, anterior sinus strong. Inner margin typically with 4 plications, which are moderately strong and occupy about the anterior third of the aperture.

The type species is a common Peronian species, but specimens from Lakes Entrance, Vic., which have been referred to *turbinata* have much stronger axial plications and other differences which imply quite a different species.

Genus SINUGINELLA, gen. nov.

Type species *Marginella inconspicua* Sowerby (Fig. 8).

Shells of small to medium size, subconical in form, with short and slightly elevated spires, white or pale ivory, smooth and highly polished. The aperture has a rounded shoulder, the outer margin nearly straight with a wide external varix, smooth within, the anterior sinus strong. The inner margin has weak and oblique, and anteriorly placed, plications, which typically number 4, but may number 3 or 5.

Sinuginella is proposed for a large group of species which are typically Australian, particularly in southern temperate waters. The form varies from typical subconical species to those which are more elongate with very short spires, but no clear line can be drawn between the two groups. Besides the type such species as *translucida* Sowerby, *humerica* Laseron, *sinuata* Laseron, *strangei* Angas, and *frequens* Laseron are typical, while the elongated, short-spired species include *olivella* Reeve, *infelix* Jousseaume, and other species. A characteristic of all species is the strong anterior sinus, and the nearest ally is probably *Mesoginella*, which differs by having plications on the shoulder. The form is also similar to the true *Marginella*, which is a large, coloured shell from West Africa, with a different texture, and probably little real relationship.

Genus KOGOMEA Habe

Kogomea Habe, 1951, p. 103, fig. 11.

Type species *Marginella novemprovincialis* Yokoyama (Fig. 9).

Small to medium subconical shells with short, elevated spires, almost identical in general characters with *Sinuginella*, but with the outer margin of the aperture strongly dentate within. Points of resemblance to *Sinuginella* are the form, the strong anterior sinus, and the weak, oblique plications on the inner margin of the aperture.

The type species came from deep water off Japan, and closely corresponds to an Australian group of which *M. stilla* (Hedley), a Peronian deep-water species, is typical. Other Australian recent species which come here are *subbulbosa* Tate and the Western Australian *patria* Cotton. Among the fossils *pera* Cotton and *sagma* Cotton are typical.

Genus SPIROGINELLA, gen. nov.

Type species *Marginella leia* Cotton (Fig. 10).

Shell broadly ovate, with slight axial plications on the shoulder, spire short. Aperture wide, shouldered posteriorly, smooth within, external varix moderate, outer margin rounded, anteriorly rounded with no sinus, inner margin with 4 plications, oblique, anteriorly placed.

The ovate form, wide aperture, and lack of an anterior sinus separates *Spiroginella* from other genera with axial plications on the shoulder. The type is a deep-water South Australian species.

Genus NEPTOGINELLA, gen. nov.

Type species *Neptoginella fascicula*, sp. nov. (Fig. 11).

Small to medium shells, ovate, with short elevated spires, the aperture often very narrow, long, with rounded shoulders, the outer margin with a slight wide varix, inwardly reflected and smooth, anterior margin rounded, without a sinus. Inner margin with 4 plications which are weak and oblique, in the type crowded at the anterior end.

This seems a natural group, nearest to *Haloginella*, from which it differs chiefly by the ovate instead of cylindrical form. A fossil species is *cassida* Cotton, which indeed is so close to *N. superstes* here described that it might almost be the same species.

Genus DEVIGINELLA, gen. nov.

Type species *Marginella brachia* Watson (Fig. 12).

Small, solid, subovate shells, with medium, elevated spires. Aperture with rounded shoulder, outer margin with slight external varix but widely reflected and dentate within, anteriorly rounded, without a sinus. Inner margin with 4 strong plications, occupying half or more of the aperture, the posterior pair transverse, the anterior pair oblique. Faint axial plications sometimes appear on the shoulder of the whorls.

Deviginella differs from such genera as *Sinuginella* and *Dictoginella* by the heavier and more ovate shell, but particularly by the absence of an anterior sinus. It resembles *Antiginella* by the heavy plications and by the aperture, but has quite a different form. Amongst southern species *victoriae* Gatliff & Gabriel comes here.

Genus HALOGINELLA, gen. nov.

Type species *Marginella mustelina* Angas (Fig. 13).

Size variable, from minute to relatively large, form cylindrical to subcylindrical, elongate, often banded with chocolate or brown, otherwise ivory or white. Spire elevated, short to medium. Aperture with rounded shoulder, outer margin with a moderate varix, smooth within, anteriorly rounded without a sinus. Inner margin with usually 4 but sometimes 3 plications which are anteriorly placed and oblique. Texture porcellanous and highly polished.

As thus defined a large group of species come within *Haloginella*, some of which, when the animal is known, may have to be separated. It is not known what significance can be attached to colour, but a superficial distinction can be made between such species as the type, which has strong, coloured bands, and those species which are white. The type lives under rocks and stones, not in sand as is usual, and the animal has been described by Hedley (1916, p. 709, Plate 1, Fig. 31).

Among foreign genera, *Volvarina* Hinds (1844, p. 75), as subsequently used by some conchologists, generally resembles *Haloginella*, but its use for Australian shells is not considered advisable. No generic description of *Volvarina* was provided by Hinds, and the name was just used in brackets in the description of the type species (by monotypy) *Marginella* (*Volvarina*) *nitida* Hinds, which came from an unknown locality. American conchologists have since, rightly or wrongly, recognized *nitida* as a West Indian species, and Habe has also used *Volvarina* for a Japanese species. It is considered, however, that the general usage of such an obscure and undefined genus is more likely to create confusion than solve any zoological problem.

Of the southern species *columnaria* Hedley & May, *tridentata* Tate, and *mixta* Petterd all have only 3 plications on the inner margin of the aperture instead of the usual 4. Again some of the northern species are relatively very large, *H. rex* being no less than 18 mm in length, while *H. infans* is only 1·5 mm. Further data are needed before it can be decided whether the group is a natural unit or whether it is heterogeneous.

Genus HYDROGINELLA, gen. nov.

Type species *Hydroginella dispersa*, sp. nov. (Fig. 14).

Shell elongated, subcylindrical, with a short elevated spire, aperture very narrow with a sloping shoulder, outer margin inwardly reflected with a dentate edge, anterior margin rounded without a sinus. Inner margin with 4 weak, oblique plications, anteriorly placed.

Hydroginella is very close to *Haloginella* in most characters, but differs by having the outer lip dentate, and by the narrow aperture, particularly anteriorly.

Genus PLICAGINELLA, gen. nov.

Type species *Marginella formicula* Lamarck (Fig. 15).

Shell relatively large, strombiform, with a long and rather slender spire, wide at the shoulder, tapering and restricted anteriorly, sculpture of axial plications on the shoulder. Aperture with a rounded shoulder, outer margin nearly straight with a strong external varix, smooth within, anterior sinus strong. Inner margin with 4 strong plications which occupy about half the aperture.

This is the first of several genera with strombiform shells which are apparently confined to southern Australia. The type comes from Maria I., Tas. The main generic characters are the form, the anterior sinus, and the axial plications on the shoulder. The sculpture separates it from such genera as *Austroginella* and *Protoginella*. Cotton (1949) makes it the basis of his Section B, which includes all shells with axial plications, but this section contains discordant elements which do not make it a natural classification. Other living species of *Plicaginella* include *georgiana* May and *praetermissa* May. The fossils *praeformicula* Chapman & Gabriel and *aldingae* Tate may also be referred here.

Genus AUSTROGINELLA, gen. nov.

Type species *Marginella muscaria* Lamarck (Fig. 16).

Medium to large, massive shells, strombiform in shape, with long spires, wide at the shoulders. Aperture relatively short, shoulders nearly square, sinuate within, outer margin nearly straight with a heavy varix, smooth within, the anterior sinus strong and deep. Inner margin with 4 heavy plications, the posterior pair transverse, occupying half or more of the aperture.

This is a well-defined and easily recognized genus which is mainly confined to southern Australia, both living and as a fossil. Amongst the recent species are *johnstoni* Petterd, *tasmanica* Tenison Woods, and *vercoi* May, while the fossil *muscaroides* Tate is very close to the type species. The nearest relative abroad is probably *Stazzania* Sacco from the European Miocene.

Genus PROTOGINELLA, gen. nov.

Type species *Marginella lavigata* Brazier (Fig. 17).

Shell of medium size, strombiform, with an elevated spire, wide at the shoulder and restricted anteriorly. Aperture with an extended and almost alate shoulder, outer margin with a heavy varix terminating at the shoulder, leaving a sulcus between it and the adjacent whorl, heavily dentate within. Anterior margin flattened without a definite sinus. Inner margin with very heavy plications, occupying half or more of the aperture, usually 4 in number but may be 5, the anterior plication very oblique, the others transverse.

This very distinctive genus contains a number of species, most of which are fossil. Typical recent species include *geminata* Hedley, while fossil species are *micula* Tate, *corpulenta* May, *atkinsoni* May, and *wentworthi* Tate. Cossman (1899, p. 87) placed *wentworthi* and *micula* with European Miocene fossils.

Genus CARINAGINELLA, gen. nov.

Type species *Marginella carinata* Smith (Fig. 18).

This genus is proposed for the so far unique type dredged in deep water off the New South Wales coast. The form of the shell and other characters are close to *Protoginella*, but the whorls are strongly carinate at the shoulder, a feature observed in no other of the family, the varix is slighter, and the dentition on the outer lip is much finer. The plications on the inner are also weaker and oblique.

Genus ALAGINELLA, gen. nov.

Type species *Marginella ochracea* Angas (Fig. 19).

Alaginella is proposed for small species like *Protoginella* in general form and with the same alate shoulder to the aperture, but more rounded anteriorly, with weaker plications on the inner margin, and with the outer margin inwardly smooth and not dentate. Recent species include *laeviplicata* Laseron, and the fossil *clisia* Cotton also conforms to the generic characters.

Genus LONGINELLA, gen. nov.

Type species *Marginella maugeana* Hedley (Fig. 20).

There is a large group of Australian species which all have biconical shells with long spires, with relatively short apertures with sloping shoulders, without an anterior sinus, and sometimes banded with brown. These can be divided readily into three, *Longinella* and *Volvarinella* with strong plications on the inner margin, occupying half or more of the length of the aperture, the upper pair transverse, the anterior pair oblique, and *Baroginella* in which the plications are weak and crowded at the anterior end. *Longinella* differs from *Volvarinella* in having the outer margin inwardly smooth, while in *Volvarinella* it is dentate.

Recent species of *Longinella* include *gabrieli* May, *cuneata* Laseron, and *kemblensis* Hedley.

Genus VOLVARINELLA Habe

Volvarinella Habe, 1951, p. 101, fig. 10.

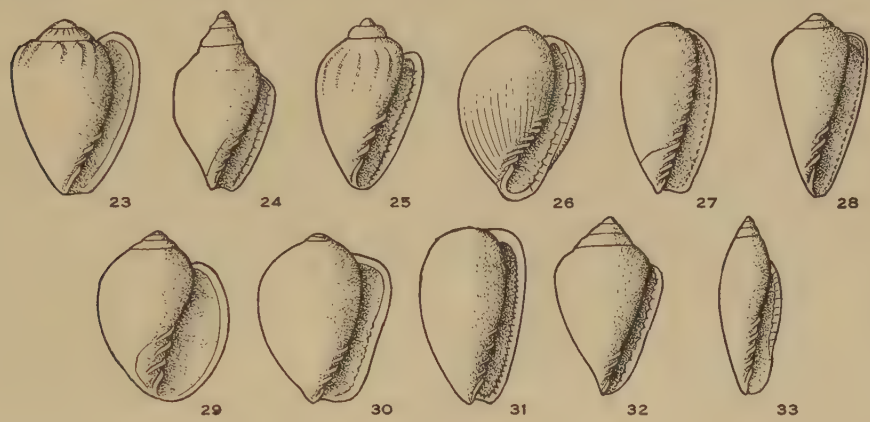
Type species *Volvarinella makiyamai* Habe (Fig. 21, after Habe).

Like *Longinella* but with the outer margin dentate within. The type species comes from Japan, and this group seems to have a wide range, both in the tropics and in temperate waters. Southern Australian species include *mayii* Tate and *allporti* Tenison Woods, and they more closely resemble the Japanese species by having coloured bands, whereas the northern Australian species discussed here are uniformly white. The outer lip is also more strongly dentate than in the Japanese species. Fossil species include *kalinae* Chapman & Crespin, *meta* Cotton, and *christa* Cotton.

Genus BAROGINELLA, gen. nov.

Type species *Baroginella infirma*, sp. nov. (Fig. 22).

Like *Longinella* and *Volvarinella* in its biconical form and long spire, but with the plications on the inner margin weak, oblique, and anteriorly placed. This difference, though apparently small, nevertheless forms a clear line of demarcation between the groups and is easily recognized. The aperture also is typically lirate within, and the lip may be faintly dentate. *Baroginella* so far is confined to northern Australia.



DEL. C. F. LASERON

Figs. 23–33 (after Cotton).—Type species of genera of Australian Tertiary Marginellidae. Fig. 23.—*Urniginella cassidiformis* (Tate). Fig. 24.—*Mioginella regula* (Cotton). Fig. 25.—*Cassoginella palla* (Cotton). Fig. 26.—*Topaginella octoplicata* (Tenison Woods). Fig. 27.—*Dentiginella matula* (Cotton). Fig. 28.—*Conuginella inermis* (Tate). Fig. 29.—*Hianoginella physa* (Cotton). Fig. 30.—*Lataginella kitsoni* (Cotton). Fig. 31.—*Vetaginella doma* (Cotton). Fig. 32.—*Stromboginella crassidens* (Chapman & Crespin). Fig. 33.—*Exiginella winteri* (Tate).

Description of Australian Tertiary Genera

Genus URNIGINELLA, gen. nov.

Type species *Marginella cassidiformis* Tate (Fig. 23).

A curious shell, broadly ovate, with short elevated spire, plications on the shoulder of the body whorl, the aperture arched at the shoulder, outer margin smooth within, anterior slightly sinuate, plications on inner margin weak and oblique.

Genus MIOGINELLA, gen. nov.

Type species *Marginella regula* Cotton (Fig. 24).

Strombiform with a long spire, in form like *Austroginella*, but with the whorls carinate and the outer margin inwardly dentate. Its nearest relative, however, is probably the living deep-water *Carinaginella*, which has a shorter spire, but may be a direct derivative.

Genus CASSOGINELLA, gen. nov.

Type species *Marginella palla* Cotton (Fig. 25).

Very like *Urniginella*, but with the aperture anteriorly rounded, the outer margin inwardly dentate, and stronger plications on the inner margin.

Genus TOPAGINELLA, gen. nov.

Type species *Marginella octoplicata* Tenison Woods (Fig. 26).

A small, broad, rotund form, with short spire, barely visible, the surface covered with fine growth lines. Aperture with rounded shoulder, outer margin inwardly dentate, rounded anteriorly, without a sinus. Inner margin with numerous plications which are thin and closely packed. There is no other known species or genus with which this can readily be compared.

Genus DENTIGINELLA, gen. nov.

Type species *Marginella metula* Cotton (Fig. 27).

Form nearly oval, spire depressed and just visible, aperture long, outer margin finely dentate within, anterior sinus strong, inner margin with numerous small plications which occupy nearly the whole length of the aperture. The nearest living representative is perhaps *Kogomea*, from which it can be distinguished by the multiplicate inner margin.

Genus CONUGINELLA, gen. nov.

Type species *Marginella inermis* Tate (Fig. 28).

Form conical with a short, elevated spire, very similar to that of a typical *Conus*, narrow anteriorly. Aperture long, outer margin nearly straight and inwardly finely dentate, anterior margin rounded without a sinus. Inner margin with 4 oblique plications anteriorly placed. The cone-like form at once distinguishes this genus from all other Marginellidae.

Genus HIANOGINELLA, gen. nov.

Type species *Marginella physa* Cotton (Fig. 29).

Form rotund, with a medium, elevated spire, the aperture rounded and widely expanded, outer margin smooth within, rounded anteriorly without a sinus, inner margin with 4 strong, oblique plications. The wide, rounded aperture at once distinguishes this from other groups, both fossil and recent.

Genus LATAGINELLA, gen. nov.

Type species *Marginella kitsoni* Chapman (Fig. 30).

Form broadly subovate with a short elevated spire, aperture with a rounded shoulder, outer margin nearly straight, dentate within, anterior sinus strong, inner margin with more than 4 small plications anteriorly placed and closely packed. The nearest living representative is *Kogomea*, of which it may be the ancestral form.

Genus VETAGINELLA, gen. nov.

Type species *Marginella doma* Cotton (Fig. 31).

Form oval, spire involute, summit domed, aperture long, shoulder arched, outer margin dentate within, anterior sinus strong, inner margin with 5 weak plications anteriorly placed. *Vetaginella* is very like the recent *Epiginella* in general characters, differing chiefly by the dentate outer margin.

Genus STROMBOGINELLA, gen. nov.

Type species *Marginella crassidens* Chapman & Crespin (Fig. 32).

Form broadly biconical with a long, elevated spire, narrowed and acute anteriorly. Aperture very narrow, outer margin nearly straight, strongly dentate within, no anterior sinus, inner margin with 4 narrow plications, crowded anteriorly. This distinctive species and genus is quite unlike any other known, either fossil or recent.

Genus EXIGINELLA, gen. nov.

Type species *Marginella winteri* Tate (Fig. 33).

Biconical, very narrow, with an elevated spire. Aperture narrow with a sloping shoulder, outer margin sinuate, dentate within, rounded anteriorly. Inner margin with 5 oblique, narrow plications. The nearest similar living group is *Volvarinella*, which is broader, with the outer margin only faintly dentate, and the plications on the inner margin 4 instead of 5. Cossman (1899, p. 86) placed the type in the section *Serrata* Jousseaume, the type of which is the recent *Marginella serrata* Gaskoin. *M. propinqua* Tate, another Australian fossil, is congeneric with *winteri*.

The Animals of Australian Marginellidae

Very little is known of the animals of Australian Marginellidae. Hedley (1916, p. 709, Plate 50, Fig. 31) described and figured the animal of *Haloginella mustelina* (Angas), Cotton (1944, p. 16) described the animal of *Protoginella weedingi* (Cotton), and D. McAlpine of the Australian Museum has now made available to the author his sketches and notes of *Haloginella mustelina* (Angas), *Euliginella angasi* (Crosse), and *Microginella nympha* (Brazier). Figures 34–36 are reproduced from Mr. McAlpine's drawings.

His notes read:

"*Marginella mustelina* [Fig. 35]. Collected at Vaucluse, Sydney, 9/2/52. Animal translucent, creamy, opaque spots, short tubercles on mantle." Hedley speaks of the mantle as papillate, and of the foot as lobed in front, and of the eyes as sessile at the outer bases of the tentacles.

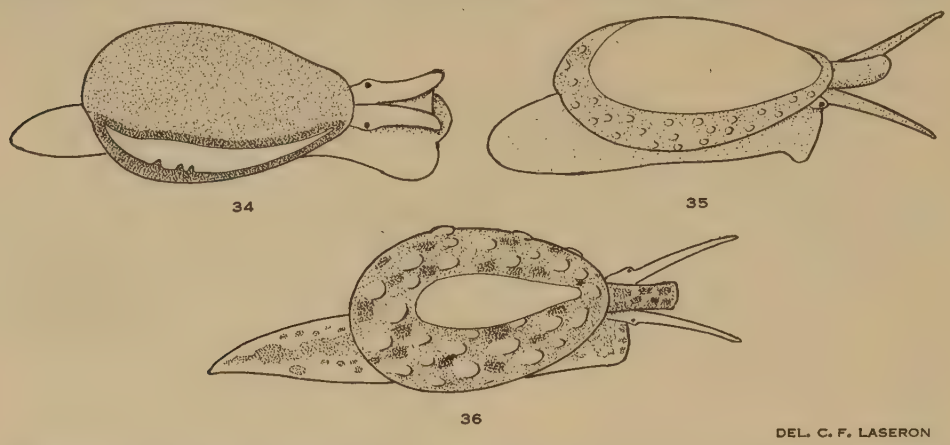
"*Marginella angasi* [Fig. 34]. Collected at Vaucluse, 9/2/52. Head and foot cream, eyes red, mantle orange, edged with deeper orange. Head with a shovel-shaped anterior expansion to which the tentacles are joined for their whole length. Eyes large, on slight swellings at the outer bases of the tentacles. Foot narrow, anterior auricles very rounded with an intermediate V-notch. Left lobe of mantle covering shell, smooth, right lobe covering varix only, smooth, with 3 short appendages. Siphon entirely absent.

"*Marginella nympha* [Fig. 36]. Collected at Long Reef, north of Sydney, 30/1/53. Cream and yellow, brown markings on mantle." To which can be added from the drawing that the mantle is covered with rounded pustules.

Cotton describes the colour of the animal of *Protoginella weedingi* (Cotton) as mainly brown, and other salient features are that the mantle is "shaggy from

translucent processes, three-branched at their extremities . . . the mantle also envelops the shell more on the front on the left and more on the back at the right".

From these limited data it is impossible to say how far animal characters will fit with the generic determinations based on the shell alone. There is, however, sufficient to show that there is considerable difference in the animals, particularly in the colour, in the development of brachial processes on the mantles, and in the head.



Figs. 34–36.—Animals of Marginellidae (after drawings by D. McAlpine). Fig. 34.—*Euliginella angasi* (Crosse). Fig. 35.—*Haloginella mustelina* (Angas). Fig. 36.—*Microginella nympha* (Brazier).

The most radical departure is in *Euliginella angasi*. This is the entire absence of a visible siphon. There must of course be an opening for the intake of sea-water to the gills, but if this is in the form of a tube, it must be very short and hidden below the edge of the shell. The fact that the tentacles are connected by a sheet of tissue throughout their length also differentiates the animal of this species not only from the few other members of the family of which the animals are known, but also from other families which are near in classification, such as the Cypraeidae and Volutidae. Much further research is needed before any definite conclusions can be reached, but at this stage even isolated observations on the animals of any Marginellidae throughout Australia will have particular value.

It is interesting to note that the author (1948, p. 46) recorded that a form of *angasi*, indistinguishable on shell characters, had a black instead of a red or orange animal. This he named var. *melania*.

B. DESCRIPTION OF SPECIES FROM THE SOLANDERIAN AND DAMPIERIAN ZOOGEOGRAPHICAL PROVINCES

All holotypes, paratypes, and specimens illustrated or recorded which are not already in the collection of the Australian Museum, Sydney, are now presented to that institution.

Two species, *Marginella valida* Watson and *M. australis* Hinds, are omitted from the description of species for reasons already given in the Discussion in Part A.

Genus EPIGINELLA, gen. nov.

Epiginella ablita, sp. nov.

Fig. 37

Shell of medium size, ovate, summit broadly domed, spire involute, but earlier whorls just discernible on extreme summit, white, smooth and polished. Aperture crescentic, beginning above the shoulder of the adjacent whorl but below the summit, shoulder rounded, outer margin with no external varix, but inwardly reflected and thickened, the edge roughened but not definitely dentate, anterior margin with a deep sinus. Inner margin multiplicate, the 2 anterior plications strongest, oblique, the 3 next just visible in front, the remainder within the aperture, 7 or 8 in all, occupying the full length of the aperture. Length 4 mm.

Locality.—Rocky I., near Cairns, Qld. (C. Hedley), holotype and 3 paratypes.

Remarks.—The nearest species to this is *concamerata* May from Tasmania, which is broader and not quite so domed at the summit.

Genus OVAGINELLA, gen. nov.

Ovaginella ovulum (Sowerby)

Fig. 38

Marginella ovulum Sowerby, 1847, p. 401, pl. 78, fig. 188. Sowerby, in Angas, 1867, p. 196.

The locality given for the type was simply Australia, but Angas recorded the species from Port Jackson, and that is now generally accepted as the type locality. The species actually has a wide range, occurring in Tasmania (Maugean), New South Wales (Peronian), and southern Queensland (Solanderian). The specimen illustrated came from 17–20 fm, Mast Head I., Capricorn Group (C. Hedley), its length 7·3 mm. Comparison with New South Wales specimens shows no difference, except that it is slightly smaller, some Peronian specimens attaining a length of 11 mm.

Genus MICROGINELLA, gen. nov.

Microginella anxia (Hedley)

Fig. 39

Marginella anxia Hedley, 1909, p. 452, pl. 43, figs. 86–7.

The type locality is 8 fm, Weary Bay, Hope Is., Qld., the length of the type 2·2 mm. The species is, however, a common and widely distributed one; specimens have been examined from Cape Sidmouth, and from 4–14 fm, Albany Passage, Thursday I., and it is also common at Darwin, extending its range into the Dampierian Province. It is constant throughout in both size and general characters, but some of the Darwin specimens are yellow-brown in colour. This recalls a similar colour variation in a beach-living shell of quite a different family, *Polinices incei* Philippi. The specimen illustrated is from Albany Passage, its length 2·2 mm. Hedley gives the number of plications on the inner margin as 5 in immature specimens but only 3 in adults, but examination shows that the full number of 5 is always present, though the posterior pair are sometimes invisible from in front.

Microginella opima, sp. nov.

Fig. 40

Shell very small, globose, body whorl inflated but narrowed anteriorly, spire involute, colour white, and surface polished. Aperture crescentic, narrow and even, commencing almost at the summit and arched above, outer margin evenly rounded with an external varix, thickened and inwardly widely reflected, the edge smooth, anterior margin narrow, rounded and without a sinus. Inner margin multiplicate, the anterior 2 plications strong, the remainder weak and barely visible from in front, occupying the full length of the aperture, the total number at least 7. Length 2·5 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley, C48715 in Australian Museum), holotype and 3 paratypes.

Remarks.—Compared with *M. anxia* this species is larger, more globose, with a different summit, the outer margin not dentate within, and the plications on the inner margin more numerous. The absence of dentition on the outer margin suggests that it may have to be removed from *Microginella*, and if so it could be referred to *Microvulina*, the type species of which comes from Japan (Habe 1951, p. 105).

Microginella vitrea, sp. nov.

Fig. 41

Shell minute, oval, completely involute, spire invisible, a callus on the summit, colourless, texture vitreous and translucent. Aperture longer than the shell, slightly arched above, even in width, outer margin rounded, inwardly reflected with a slightly dentate edge, rounded anteriorly. Inner margin with oblique plications, only 4 visible, others if they exist within the aperture and obscured by sand grains. Length 1·3 mm.

Locality.—Port Curtis, Qld. (J. Laseron), holotype and 1 paratype.

Remarks.—This is the smallest of any of the species studied; it is narrower and more oval than either of the preceding species, and can also be distinguished by its translucent, vitreous texture.

Genus PHYLOGINELLA, gen. nov.

Phyloginella simplex, sp. nov.

Fig. 42

Shell very small, broadly ovate, with a depressed, dome-shaped spire, visible from in front, colour white, smooth and polished. Aperture long, beginning above the shoulder of the adjacent whorl but below the suture, of nearly even width widening only slightly anteriorly, shoulder rounded, outer margin nearly straight, external varix slight, but inwardly reflected and smooth, anterior margin with a slight sinus and nearly truncate. Columella pillar broad and rounded, inner margin with 4 plications, weak, oblique and anteriorly placed, 3 only visible from in front, the posterior plication very faint and within the aperture. Length 2·7 mm.

Locality.—Thursday I. (J. Laseron), holotype and 6 paratypes.

Remarks.—This is the smallest of the 3 species here discussed, and differs also by the form and shallower anterior sinus.

Phyloginella pachia (Watson)

Fig. 43 (after Watson)

Marginella (*Glabella*) *pachia* Watson, 1886, p. 265, pl. 16, fig. 5.

The type locality is 155 fm, off Raine I., the length given 0·14 in. or approximately 3·5 mm. This species has not been recorded since its discovery, but the very tumid form should make its future recognition easy.

Phyloginella compressa, sp. nov.

Fig. 44

Shell of medium size, ovate, with a depressed, dome-shaped spire, just visible from in front, colour white, smooth and polished. Aperture long, beginning just above the shoulder of the adjacent whorl, narrow above, widening anteriorly, shoulder rounded, outer margin with no discernible varix, but inwardly reflected and smooth, anterior sinus strong. Inner margin with 4 plications, thin and oblique, occupying about one-fourth of the aperture, the posterior plication barely visible from in front. Length 4·5 mm.

Locality.—Wreck Reef, Coral Sea (C. Hedley, C32404 in Australian Museum), holotype and 1 paratype.

Remarks.—This, the type of the genus, is the largest of the 3 species here discussed, and differs also in the form.

Genus EULIGINELLA, gen. nov.

Euliginella angasi (Crosse)

Figs. 45–48

Marginella angasi Crosse, 1870, p. 304. Hedley, 1914, p. 726, pl. 82, fig. 66.
Marginella minima Petterd, 1884, p. 144.
Marginella simsoni Tate and May, 1900, p. 92.
Marginella shorehami Pritchard and Gatliff, 1899, p. 179, pl. 20, fig. 2.
Marginella amphora Laseron, 1948, p. 46, pl. 6, fig. 43.

The lengthy synonymy of this species is due to its extreme variability and to its extensive range. The variability, however, is not localized, as the various forms exist in the one locality, and there is no tendency to form geographical races. The range to date has been recorded over the southern provinces—Flindersian, Maugean, and Peronian—and it is now extended to the Solanderian and Dampierian as well, from the cool-temperate waters of Tasmania to the tropics at Darwin. A long series from Darwin, where it is common, shows all the extremes of variation, so much so that at first sight several species seemed indicated. Close examination showed, however, that there was a perfect intergrading linking the most extreme forms. The main variations are in the relative width of the shell, in the curve of the body whorl, and also in the degree of arching of the shoulder of the aperture, this arching being sometimes high above the summit (Figs. 45, 48) and at other times practically

level (Fig. 46). The high-arched forms from the Peronian Province had previously been separated by the author (1948) as *Marginella amphora* but this name is now withdrawn. Figures 45 and 46 are specimens from Darwin and show about the extreme of variation. Each is 2·2 mm in length. Figure 48 is a specimen from Torres Strait, and is slightly larger, being 2·5 mm in length. This form can also be matched from Darwin and elsewhere. Specimens from Port Curtis, Qld., match the Darwin specimens in size, and most are close to that of Figure 45. Specimens from 17–20 fm, Mast Head I., show the same variability but are smaller, ranging from 1·4 to 1·6 mm in length. A character which can be misleading on superficial examination is the number of plications on the inner margin. These are thin and oblique, and from the front 2 or 3 only can usually be seen. Within the aperture they are sharp and raised, occupying the whole length, and numbering as many as 10. Figure 47 is of a shell from Darwin with the aperture partly broken away, and shows this clearly.

Euliginella melwardi, sp. nov.

Fig. 49

Shell of medium size, relatively large for the genus, subconical in form, broad at the shoulder, flattened above and tapering sharply anteriorly, spire depressed, hardly visible from in front, colour white. Aperture long and of even width, the shoulder arched above the summit, outer margin nearly straight, without a varix, inwardly reflected and smooth, anterior margin narrow and rounded. Inner margin with oblique, narrow plications, only the anterior ones visible from in front, but occupying nearly the whole length within the aperture, 8 detected. Length 3·8 mm.

Locality.—At 8–9 fm, off Point Charles, Darwin (Mel. Ward), holotype and 3 paratypes.

Remarks.—This can readily be separated from *E. angasi* by the conical shape and even flatter summit, and particularly by the much larger and more massive shell.

Genus KOGOMEA Habe

Kogomea striata, sp. nov.

Figs. 50, 51

Shell small, ovate, spire short and elevated, colour white, surface smooth and polished. Aperture long, even, commencing above the shoulder of the adjacent whorl, shoulder rounded and sloping, outer margin medially sinuate, without an external varix, inwardly narrowly reflected, the edge finely dentate, striate within the aperture, anterior margin with a strong sinus. Inner margin with oblique, weak, and thin plications, 3–4 visible from in front, others within the aperture, 6–7 in all, occupying about half the total length, but the posterior plications very faint even when the aperture is broken away. Length 2·7 mm.

Localities.—Michaelmas Cay (T. Iredale), common, holotype and 18 paratypes selected; Bowen, Qld. (J. Laseron).

Remarks.—This species resembles in form the Peronian deep-water *K. stilla* (Hedley), from which it differs by being smaller and narrower, by being striate within the aperture, and by the weaker and more numerous plications on the inner margin.

Genus NEPTOGINELLA, gen. nov.

Neptoginella fascicula, sp. nov.

Fig. 52

Shell of medium size, ovate, body whorl swollen and restricted anteriorly, the regular curvature of the outer margin of the aperture combined with this giving the whole a slightly bent appearance, spire short, elevated, and broadly dome-shaped, colour white, texture porcellanous and polished. Aperture long, beginning at the suture, very narrow and even in width, shoulder rounded, outer margin rounded with a wide external varix, inwardly thickened and smooth, anterior margin narrow and rounded, without a sinus. Inner margin with 4 plications which are thin and oblique, and closely crowded at the anterior end. Length 4·8 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley, C48716 in Australian Museum), holotype and 7 paratypes.

Remarks.—There is no other Australian species with which this can readily be compared. The slightly bent appearance of the anterior end gives a distinct facies, and the crowding of the thin plications on the inner margin anteriorly is another good recognition point.

Neptoginella tropica, sp. nov.

Fig. 53

Shell small, ovate, broad above, tapering and slightly restricted anteriorly, spire short and elevated, colour white, texture porcellanous and polished. Aperture long, commencing above the shoulder of the adjacent whorl at the suture, narrow and nearly even in width, widening only slightly anteriorly, shoulder rounded, outer margin nearly straight and medially very slightly sinuate, external varix wide, inwardly thickened and reflected, smooth, anterior margin rounded. Inner margin with 4 plications, moderately strong and oblique, occupying about one-third the total length of the aperture. Length 3·4 mm.

Localities.—Darwin (J. Laseron), holotype and 2 paratypes; Michaelmas Cay (T. Iredale); 5–8 fm, Murray I. (C. Hedley, C48737 in Australian Museum).

Remarks.—This is a smaller species than *N. fascicula*, it has a different contour, and the plications on the inner margin are stronger and not crowded at the anterior end. The Michaelmas Cay specimens are rather smaller than the type, averaging about 3 mm in length.

Neptoginella superstes, sp. nov.

Fig. 54

Shell very small, subovate, nearly oval, anteriorly wider than usual, spire short and elevated, colour white, texture rather vitreous and translucent. Aperture long, narrow above, widening anteriorly, commencing just below the suture, shoulder rounded, outer margin flattened, medially sinuate, with no apparent external varix, inwardly reflected, the reflection wider posteriorly, smooth, anterior margin rounded. Inner margin with 4 plications, anteriorly placed, thin and oblique, the posterior

plication barely visible from in front, the anterior plication bordering the columella. Length 2·6 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group, Qld. (C. Hedley, C19538 in Australian Museum), holotype and 2 paratypes selected from full tube.

Remarks.—This interesting species is very close to the Tertiary fossil *N. cassida* (Cotton) from 400 ft in a bore on the Adelaide Plains, and from the figures might almost be taken for that species, except that *cassida* is more than twice the size and has stronger plications on the inner margin. There is of course a vast disparity in age.

Genus DEVIGINELLA, gen. nov.

Deviginella brachia (Watson)

Figs. 55 (after Watson), 56

Marginella (*Glabella*) *brachia* Watson, 1886, p. 268, pl. 16, fig. 4.

The type locality is 155 fm off Raine I., the length of the type 0·11 in. or approximately 2·8 mm. Specimens from Facing I., Qld., collected by K. L. Kesteven (C44469 in Australian Museum) agree almost exactly with Watson's figure except that the shoulders of the aperture are slightly more sloping, and that the specimens are larger, that figured (Fig. 56) being 3·7 mm in length. Other mature specimens are, however, nearer the type in size, averaging about 3·3 mm. Without actual comparison with the type it is difficult to determine if the very slight differences have any racial or specific value.

The general characters of the species correspond with those already outlined in the generic description, and can be appreciated best by study of the figures.

Deviginella maxilla, sp. nov.

Fig. 57

Shell minute, broadly ovate, solid, narrow anteriorly, spire short but elevated, colour of holotype white but one of the paratypes yellow, surface highly polished. Aperture narrow, beginning just below the suture, shoulder rounded and sloping, outer margin rounded with no appreciable external varix, but inwardly broadly reflected with a dentate edge, greatly restricting the apertural opening, anterior margin narrow and rounded. Inner margin with 4 plications which are heavy and thick, occupying about half the aperture, the anterior plication oblique, the others transverse. Length 2 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group (C. Hedley, C19537 in Australian Museum), holotype and 2 paratypes.

Remarks.—This striking little species conforms to all the characters defined in the genus and is close to the type *D. brachia*, but is much smaller and relatively much broader.

Deviginella modulata, sp. nov.

Fig. 58

Shell small, ovate, evenly rounded and not shouldered at the periphery, tapering anteriorly, spire short and elevated, white, texture slightly translucent.

Aperture long, widening anteriorly, commencing just below the suture, shoulder sloping, continuing the line of the spire, outer margin only slightly curved, with a wide external varix, inwardly thickened and bearing about 12 small denticles, anterior margin rounded. Inner margin with 5 plications in all, occupying about half the aperture, oblique, the anterior plication strong, the next 3 subequal, the 5th nearly within the aperture and just visible from in front. Length 3·6 mm.

Locality.—At 8–9 fm, Point Charles, Darwin (Mel. Ward), holotype and 3 paratypes.

Remarks.—This is a rather less solid shell than *D. brachia*, it is narrower with a different contour, the aperture is wider, the plications on the inner margin are not transverse and number 1 more.

Genus HALOGINELLA, gen. nov.

Haloginella agata, sp. nov.

Fig. 59

Shell small, subconical, with a short, broad, elevated spire, smooth and highly polished, colour pale yellow-brown with darker and very pale bands. Aperture long, beginning just above the suture, shoulder sloping, outer margin nearly straight, with a narrow external varix, inwardly reflected and smooth, anteriorly rounded without a sinus. Inner margin with 4 plications, which are thin, oblique, and anteriorly placed, the anterior pair the strongest. Length 5 mm.

Locality.—Coquet I., Qld. (C. Hedley, C49502 in Australian Museum), holotype only.

Remarks.—The holotype was labelled *Marginella mustelina* Angas, and was probably the specimen on which *mustelina* had been recorded from Queensland. The colouring is certainly similar, but *agata* has quite a different contour, it is less cylindrical, and the aperture has a more sloping shoulder and is wider anteriorly.

Haloginella agatha, sp. nov.

Fig. 60

Shell of medium size, cylindrical, elongate, spire short, broad and elevated, white or ivory in colour, sometimes with faint brown bands. Aperture long, widening anteriorly, shoulder rounded, beginning above the suture, outer margin slightly sinuate, with a slight but broad external varix, inwardly reflected and smooth, rounded anteriorly without a sinus. Inner margin with 4 plications, anteriorly placed, thin and oblique, the posterior pair thinner than the others. Length 7·3 mm.

Locality.—Murray I. (C29612 in Australian Museum), common, holotype and 2 paratypes selected.

Remarks.—This is another species which resembles the Peronian *mustelina* Angas, but it again has a different contour, and the shoulder is more sloping. The differences are apparent when the two species are studied side by side.

Haloginella diminuta, sp. nov.

Fig. 61

Shell small, cylindrical, spire very short and broad, elevated, pure white, texture porcellanous and highly polished. Aperture long, narrow posteriorly, widening anteriorly, shoulder arched, outer margin nearly straight, with a slight external varix, inwardly reflected and thickened, anterior margin flattened but without a sinus. Inner margin with 4 plications, anteriorly placed, oblique, the posterior plication weak, the middle 2 elevated and crossing the columella, the anterior plication bordering the aperture. Length 3·8 mm.

Localities.—Cape Sidmouth, Qld. (A. U. Henn, C2638 in Australian Museum), holotype and 3 paratypes; 15–20 fm, Point Charles, Darwin (Mel. Ward), 4 specimens.

Remarks.—This is the closest of the northern species in form to *mustelina* Angas, but it is only half the size, the spire is shorter, and it lacks the distinctive colouring. From the material available it is very constant, and no difference at all could be detected between the Queensland and the Darwin specimens.

Haloginella augerea, sp. nov.

Fig. 62

Shell relatively large, subcylindrical, summit flattened with a short, domed, and hardly elevated spire, white, porcellanous and highly polished. Aperture nearly as long as the whole shell, beginning at the suture, widening anteriorly, shoulder rounded, outer margin nearly straight, with a wide, rounded, but not clearly defined external varix which fades at the shoulder, inwardly reflected and smooth, anterior margin wide and rounded. Inner margin with 4 oblique plications, anteriorly placed, the posterior plication thin and barely visible from in front, the others stronger. Length 9 mm.

Locality.—Keppel Bay, Qld. (J. Laseron), holotype and 2 paratypes.

Remarks.—This species is rather doubtfully referred to *Haloginella*, though it conforms fairly well to the characters of the genus as defined; but the flattened summit and high-shouldered whorls give it a rather different facies, which suggests that it may have other relationship. The species itself is so distinctive that there should be little difficulty in its future recognition.

Haloginella keppelensis, sp. nov.

Fig. 63

Shell large, subcylindrical, with a broad spire of moderate length, domed at the summit, sutures just discernible, colour a pale ivory, surface porcellanous and highly polished. Aperture commencing with a sloping shoulder from below the suture, very narrow posteriorly but widening anteriorly, outer margin medially sinuous with an ill-defined external varix, inwardly reflected, rounded anteriorly without a sinus. Inner margin with 4 oblique plications, anteriorly placed, the posterior pair weak, the anterior pair strong. Length 12·5 mm.

Locality.—Keppel Bay (J. Laseron), holotype and 1 paratype.

Remarks.—This is one of the few Australian species above 12 mm in length, and amongst these its characters are distinctive. Its nearest relation is perhaps the still larger *H. rex*, hereafter described, and while both are tentatively placed in *Haloginella* it is possible that they are more closely linked with one of the groups of foreign species yet to be named. A third species which also seems closely related to these is *H. torresina*, which is next described. This, however, is only about half the size.

Haloginella torresina, sp. nov.

Fig. 64

Shell of medium size, subcylindrical, with a blunt spire of moderate length, colour a very pale cream, texture porcellanous and highly polished. Aperture long, beginning below the suture, narrow posteriorly, widening anteriorly, shoulder sloping, outer margin straight, external varix slight, inwardly reflected, smooth, anteriorly rounded. Inner margin with 4 plications, anteriorly placed, oblique, thin and sharp, the 2 anterior ones strongest. Length 6 mm.

Localities.—Thursday I. (J. Laseron), holotype; 4–14 fm, Albany Passage (C. Hedley).

Remarks.—The closest species to this is *H. keppelensis*, which, however, is twice the size and has a different contour, best appreciated by comparison of the figures.

Haloginella rex, sp. nov.

Fig. 65

Shell relatively very large, subcylindrical, elongated, tapering anteriorly, with a medium, rather sharp spire, in colour and texture like polished ivory. Aperture long, with a sloping shoulder, beginning at the suture, narrowed posteriorly, widening anteriorly, outer margin medially slightly sinuous, external varix slight but wide, inwardly reflected, smooth, anteriorly rounded without a sinus. Inner margin with 4 oblique plications, sharp and raised, occupying about two-fifths of the aperture. Length 18 mm.

Locality.—At 15–20 fm, off Point Charles, Darwin (Mel. Ward), holotype and 2 paratypes.

Remarks.—This is by far the largest of all the species here discussed, in fact of all the Australian Marginellidae, approximating in size to some of the African species, though one of these is over 2 in. in length. In form it approximates to *H. torresina*, but it is three times the size and differs slightly in contour.

Haloginella infans, sp. nov.

Fig. 66

Shell minute, cylindrical, spire short and blunt, only slightly elevated, white or colourless, texture rather vitreous and slightly translucent. Aperture nearly even in width, widening only at anterior end, beginning below the suture, shoulder rounded and slightly arched, outer margin nearly straight, medially very slightly sinuous,

inwardly reflected, smooth, anteriorly rounded. Inner margin with 4 oblique, thin plications, the anterior one much the strongest. Length 1·5 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group (C. Hedley, C21764 in Australian Museum), holotype and 1 paratype selected from 12 specimens, most of which had deteriorated.

Remarks.—This is easily the smallest of the group, and such is its disparity in size compared with *H. rex* that it is difficult to reconcile them as congeneric; yet *infans* conforms in all particulars to the generic description as given, except that the texture is rather more vitreous than in the other species.

Genus HYDROGINELLA, gen. nov.

Hydroginella dispersa, sp. nov.

Fig. 67

Shell of medium size, subcylindrical, long and slender, tapering anteriorly, with an elevated spire of moderate length showing 3 whorls with distinct sutures, white, porcellanous and highly polished. Aperture long and crescentic, very narrow, even in width, beginning above the shoulder of the adjacent whorl and just below the suture, shoulder rounded and sloping, outer margin rounded, with a broad external varix, and reflected inwards with a finely dentate edge, anteriorly rounded and without a sinus. Inner margin with 4 weak and oblique plications, packed anteriorly, occupying only about one-sixth of the aperture. Length 5·5 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley), holotype.

Remarks.—This species can only be compared with the various species of *Haloginella*, from all of which it differs in that it is narrower and has a narrower aperture, and generically by being dentate on the outer margin.

Genus AUSTROGINELLA, gen. nov.

Austroginella queenslandica, sp. nov.

Fig. 68

Shell of medium size, strombiform, subangled at the shoulder, spire high and elevated, white, texture porcellanous and polished, but with faint, irregular plications or undulations on the shoulder. Aperture beginning at the suture, of even width, rounded and pronounced, outer margin curved, with a narrow external varix, inwardly widely reflected with a finely dentate edge, anterior margin with a strong sinus. Inner margin with 4 heavy subequal plications which are slightly oblique and occupy about one-half the aperture. Length 4·7 mm.

Localities.—Curtis I., Port Curtis, Qld. (J. Laseron), common, holotype and 20 paratypes; Caloundra, Qld. (C12593 in Australian Museum); 17–20 fm, Mast Head I., Capricorn Group (C. Hedley).

Remarks.—Though most of the characters conform to *Austroginella*, it differs from all other species of that genus by the dentate outer margin, and should other species be discovered this could justify further generic separation. It is also smaller

than any of the other species, in form approaching closest to the southern species *tasmanica* Tenison Woods.

Genus PROTOGINELLA, gen. nov.

Protoginella lavigata (Brazier)

Fig. 69

Marginella lavigata Brazier, 1877, p. 225.
Marginella baudinensis Smith, 1899, p. 208, fig. 2.
Marginella laevigata Brazier (emend.), in Hedley, 1901, pl. 26, fig. 5.

The name of this species as published by Brazier is *lavigata*, but Hedley when he figured it in 1901 altered the spelling to *laevigata*, by which it has since been known. It is considered that the original name as printed must stand even if the author had intended otherwise, and irrespective of Greek or Latin roots which might or might not be apropos. Smith can well be excused for overlooking Brazier's name when he proposed his species, as at the time the species had not been figured and the type was in Australia.

This prominent and well-defined species occurs in many localities on the Queensland coast, is found in Torres Strait, and extends well into the Dampierian Province, occurring at Darwin, while Smith's *baudinensis* was described from tropical Western Australia. The species shows little variation throughout its range. The specimen illustrated is from 15–20 fm, off Point Charles, Darwin, collected by Mel. Ward, and is 7 mm in length. A noticeable feature, apart from the distinctive form and heavily dentate outer margin, is the heavy, transverse plications on the inner margin.

Protoginella praeterea, sp. nov.

Fig. 70

Shell of medium size, heavy, strombiform, broad at the periphery, sharply restricted anteriorly, with a long, elevated spire of 3 whorls, the initial whorl domed, sutures distinct, colour white, texture porcellanous and highly polished. Aperture relatively short, narrow, shoulder winged, channelled posteriorly, outer margin slightly curved with a narrow external varix which ends abruptly at the shoulder, internally thickened, the edge nearly truncate and crossed by about 13 heavy plications which terminate in teeth within the aperture. Anterior margin flattened, but without a sinus. Inner margin with 5 plications occupying four-fifths of the aperture, the anterior plication oblique and bordering the aperture, the other 4 heavy and transverse, well developed within the aperture, the posterior plication barely visible from in front. Length 6 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group (C. Hedley, C21767 in Australian Museum), holotype.

Remarks.—The so far unique holotype is so distinctive that its specific separation is justified though founded on a single specimen. It can be readily separated from *lavigata* by the narrower form and longer spire, and more particularly by the extra plication on the inner margin.

Genus ALAGINELLA, gen. nov.

Alaginella albino, sp. nov.

Fig. 71

Shell small, strombiform, spire elevated, long, of 3 whorls, the apex domed, body whorl wide at the periphery, restricted anteriorly, colour pure white, texture porcellanous and highly polished. Aperture about two-thirds of total length, with a posterior sinus, shoulder widely extended, slightly oblique, rounded, outer margin slightly curved, with an external varix, inwardly widely reflected and smooth, greatly restricting the width of the aperture, anterior margin rounded without a sinus. Inner margin with 4 plications, occupying more than half the aperture, the 3 anterior ones very strong and slightly oblique, the posterior plication well separated, not so strong, often invisible from in front, but well developed within the aperture. Length 3·4 mm.

Locality.—At 4–14 fm, Albany Passage (C. Hedley), holotype and 4 paratypes.

Remarks.—This is very close to the southern species *A. ochracea* (Angas), but is slightly smaller and relatively slightly broader, the aperture is narrower, and the texture and colour are different, *ochracea* being uniformly yellow whereas *albino* is pure white and more highly enamelled. The differences, though slight, are uniform.

Alaginella pygmora, sp. nov.

Fig. 72

Shell very small, strombiform, spire elevated, long, of 3 whorls, apex domed, body whorl broad at the periphery, only slightly restricted anteriorly, colour pale ochre, texture slightly translucent, shining but not highly polished. Aperture relatively long, about three-quarters of total length, shoulder widely extended and almost square, with a posterior sinus, outer margin slightly rounded with a strong external varix, inwardly widely reflected and smooth, anterior margin rounded. Inner margin with 4 plications, occupying about half the aperture, the anterior 3 strong and slightly oblique, the posterior plication weaker and more within the aperture, but visible from in front. Length 2·5 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group (C. Hedley), holotype.

Remarks.—This species is close in colour and texture to *A. ochracea* (Angas), but is much smaller than either *ochracea* or *albino*, is relatively broader, the aperture longer, the spire shorter, the shoulder of the aperture more widely angled, and the body whorl less restricted anteriorly.

Genus LONGINELLA, gen. nov.

Longinella tropica, sp. nov.

Fig. 73

Shell of medium size, biconical, medially broad, spire long and elevated, summit narrowly domed, of 3 whorls, sutures impressed, the upper 2 whorls honey-coloured, remainder of shell white, porcellanous and highly polished. Aperture relatively

short, wide, with a wide posterior sinus, shoulder sloping almost in the line of the spire, the outer margin regularly rounded, with an external varix, inwardly reflected, thickened and rounded, smooth, anterior margin broadly rounded. Inner margin with 4 strong and oblique plications, occupying more than half the aperture. Length 6 mm.

Locality.—Off Horsey I., Qld. (C. Hedley, C15117 in Australian Museum), holotype.

Remarks.—This is the first of a group of Queensland species, and conforms well to the generic description as exemplified in the type *L. maugeana* (Hedley); but none of the tropical species has the colour bands characteristic of most of those from the south.

Longinella arvina, sp. nov.

Figs. 74, 75

Shell of medium size, biconical, spire long and elevated, of 3 whorls, summit broad, sutures hardly distinguishable, white, porcellanous and highly polished. Aperture about three-fifths of total length, relatively narrow, with a posterior sinus, shoulder sloping almost in line of spire, aperture evenly rounded, external varix strong, inwardly reflected and thickened, edge rounded and smooth, anteriorly rounded. Inner margin with 4 strong oblique plications, occupying about three-fifths of the aperture. Length 5·5 mm, aperture 3·5 mm.

Locality.—At 4–14 fm, Albany Passage (C. Hedley), holotype (Fig. 74), and 2 other specimens (Fig. 75).

Remarks.—This species is very close to *L. tropica*, but is narrower and has a slightly different contour, and the aperture is narrower and relatively longer. The 2 other specimens have not been designated paratypes, as they are slightly smaller, their length being only 3·7 mm, and they each have what appears to be an indistinct spur posteriorly within the aperture.

Longinella tollere, sp. nov.

Fig. 76

Shell of medium size, biconical, medially broad, spire long and elevated, of 3 whorls, apex rather narrow, colour pale buff, texture polished but slightly translucent. Aperture long for the genus, about three-quarters of total length, moderately wide and even, shoulder sloping but slightly protruding, with a posterior sinus, outer margin nearly straight with a very heavy external varix, inwardly reflected and smooth, anteriorly rounded without a sinus. Inner margin with 4 plications, occupying about half the aperture, the anterior pair very strong and oblique, the posterior pair not so strong and nearly transverse. Length 5 mm, aperture 3·8 mm.

Locality.—At 17–20 fm, Mast Head I., Capricorn Group (C. Hedley), holotype.

Remarks.—This has a different contour from both the preceding species, the aperture is relatively longer and the shoulder protrudes more. The colour and texture are also slightly different.

Genus VOLVARINELLA Habe

Volvarinella walkeri (Smith)

Fig. 77

Marginella walkeri Smith, 1899, p. 208, fig. 1.

The type locality is at 11–34 fm, Baudin I. and Holothurian Banks, north-western Australia, the dimensions given being length 12 mm and width 5 mm. Specimens from 15–20 fm, off Point Charles, Darwin, collected by Mr. Mel. Ward, are practically identical with Smith's description and figure, except that they are slightly smaller and relatively a little broader, that figured being 8·7 mm in length and 4·4 mm in width. The denticles on the inner margin number 13, in Smith's description they are 12, which is very close. Such differences are well within the reasonable limits of individual variation. This is a large and robust species with well-marked characters which make its recognition easy.

Volvarinella fortis, sp. nov.

Fig. 78

Shell small, broadly biconical, solid, spire elevated, of 3 whorls, sutures impressed, apex broad and domed, colour pale ivory or white, texture porcellanous and polished. Aperture long for the genus, about two-thirds of total length, with a posterior sinus, outer margin rounded without a distinct shoulder, with a narrow, raised external varix, thickened and broadly reflected within, the edge with about 6 raised denticles, the posterior one the largest, progressively decreasing in size anteriorly, the anterior margin rounded. Inner margin with 4 plications occupying two-thirds of the aperture, the anterior pair oblique and very strong, the posterior pair transverse. Length 2·9 mm.

Localities.—At 5–8 fm, Murray I. (C. Hedley and A. McCulloch, C48615 in Australian Museum), holotype and 2 paratypes; 17–20 fm, Mast Head I. (C. Hedley, C19532 in Australian Museum).

Remarks.—This solid little species is relatively broader, with a shorter spire, longer aperture, and the denticles on the outer margin larger and fewer, than in the other species here discussed. The strong plications on the inner margin also occupy a greater proportion of the aperture. Specimens from Mast Head I. are rather smaller than the type, averaging about 2·4 mm in length, and the denticles on the outer margin are not so large.

Volvarinella insecta, sp. nov.

Fig. 79

Shell very small, biconical, spire elevated and long, whorls 3, sutures faintly impressed, apex broad and domed, colour white, texture semiporcellanous and slightly translucent. Aperture relatively short, little more than half of the total length, with a posterior sinus, shoulder sloping almost in line of spire, outer margin with a slight external varix, rounded, inwardly widely reflected, the edge dentate with an indistinct spur at the posterior end, anterior margin rounded. Inner margin with

4 strong plications, occupying more than half the aperture, the anterior pair oblique, the posterior pair transverse. Length 2·5 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley and A. McCulloch, C48316 in Australian Museum), holotype and 4 paratypes.

Remarks.—This is the smallest and narrowest of the species, and though it differs in detail only from those already discussed, it can easily be distinguished by size alone.

Volvarinella alta (Watson)

Figs. 80 (after Watson), 81

Marginella (*Glabella*) *alta* Watson, 1886, p. 268, fig. 2.

The type locality is 155 fm, off Raine I., the length given being 0·15 in. or approximately 3·7 mm. It is now identified with a little doubt, but specimens from 5–8 fm, Murray I. (C48723 in Australian Museum), correspond reasonably well with Watson's figure and description, though they are a little smaller, that figured (Fig. 81) being 3·2 mm in length. A copy of Watson's figure (Fig. 80) is here reproduced for comparison. It is very close to *V. walkeri* (Smith), but is less than half the size, has a slightly longer spire, and has relatively a slightly shorter aperture.

Genus BAROGINELLA, gen. nov.

Baroginella infirma, sp. nov.

Fig. 82

Shell of medium size, biconical, narrow and elongate, spire long and elevated, summit domed, sutures distinct, white, texture porcellanous and highly polished. Aperture little more than half the total length, beginning at the periphery of the adjacent whorl, very narrow posteriorly and widening anteriorly, shoulder sloping almost in the line of the spire, outer margin nearly straight and medially sinuous, with no appreciable external varix, but inwardly thickened and reflected, the edge minutely denticulate, striate within the aperture, anterior margin rounded without a sinus. Inner margin with 4 thin and oblique plications, close together at the anterior end, the posterior plication barely discernible from in front. Length 4·5 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley and A. McCulloch, C48710 in Australian Museum), holotype and 5 paratypes.

Remarks.—The narrow form, the very narrow sloping shoulder, and the closely packed plications on the inner margin should facilitate the recognition of this species.

Baroginella volunta, sp. nov.

Fig. 83

Shell small, biconical, spire long and elevated, with a blunt, domed apex, 3 whorls visible, but only the lower suture clearly defined, colour white, texture porcellanous and highly polished. Aperture about two-thirds of total length, narrow posteriorly and widening anteriorly, the shoulder sloping but extending beyond the line of the spire, outer margin medially sinuous, without an external varix, but inwardly reflected, the reflection widest on the posterior half and thinning anteriorly,

the edge smooth, the anterior margin rounded. Inner margin with 4 plications, occupying about two-fifths of the aperture, oblique but stronger than in *B. infirma*, the posterior plication transverse. Length 3·5 mm.

Localities.—At 5–10 fm, Hope Is., Qld. (C. Hedley, C27290 in Australian Museum), holotype and 1 paratype; 5–8 fm, Murray I. (C. Hedley and A. McCulloch), 7 specimens.

Remarks.—This is rather doubtfully placed in *Baroginella* as in many characters it comes close to *Longinella*, but is provisionally retained in *Baroginella* because the plications occupy less than half the aperture. It cannot be readily confused with either of the 2 species of *Baroginella* here discussed.

Baroginella attentia, sp. nov.

Fig. 84

Shell of medium size, biconical, the maximum diameter about one-fourth from the summit, spire elevated, the lower suture barely distinguishable, white, texture porcellanous and highly polished. Aperture about two-thirds of total length, beginning just below the periphery of the adjacent whorl, shoulder sloping in the line of the spire, very narrow posteriorly, widening anteriorly, outer margin nearly straight, medially very slightly sinuous, without an external varix, but inwardly thickened and reflected, the edge with no discernible denticulation, but the aperture faintly striate within anteriorly, anterior margin rounded. Inner margin with 4 narrow and oblique plications, packed closely anteriorly, the posterior plication faint and just discernible. Length 6 mm.

Locality.—At 5–8 fm, Murray I. (C. Hedley and A. McCulloch), holotype and 2 paratypes.

Remarks.—This is close in general appearance to *B. infirma*, but is larger, with quite a different contour, the aperture relatively longer, and the striations within it not so distinct.

Corrections to Species of the Peronian Province

In the discussion on *Euliginella angasi* (Crosse), *Marginella amphora* Laseron has already been withdrawn as a synonym of *angasi*.

Kogomea royana, nom. nov., is now also proposed for *Marginella quinqueplicata* Laseron (1948, p. 41, Plate 5, Fig. 22), preoccupied by *Marginella quinqueplicata* Lamarck. The species is now renamed after Mr. Roy Bell who collected it at Twofold Bay, N.S.W.

Acknowledgments

In the compilation of this paper the author is greatly indebted to the authorities of the Australian Museum, particularly the Director, Dr. J. W. Evans, and the Conchologist, Dr. D. McMichael, for making available the library and collections of the Museum, and to Mr. D. McAlpine for the use of his drawings and notes on the animals of some of the Marginellidae. To his son, John Laseron, goes much of the credit for careful collecting from Darwin and a number of localities in Queensland.

And to Mr. Tom Iredale particularly, thanks are again due for the unselfish way he has cooperated, sorted specimens from Michaelmas Cay and other localities, and assisted throughout with advice culled from his vast knowledge and experience.

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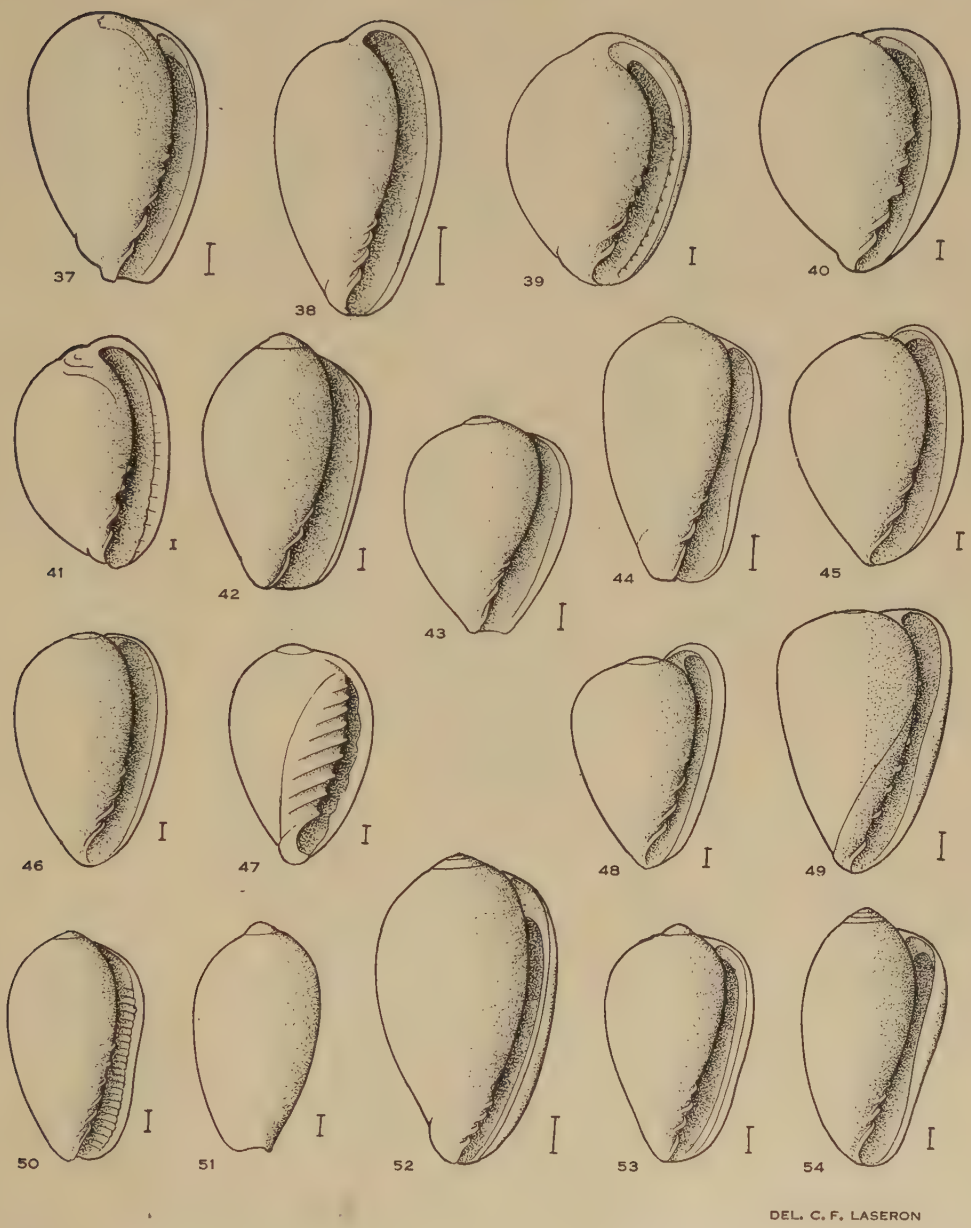
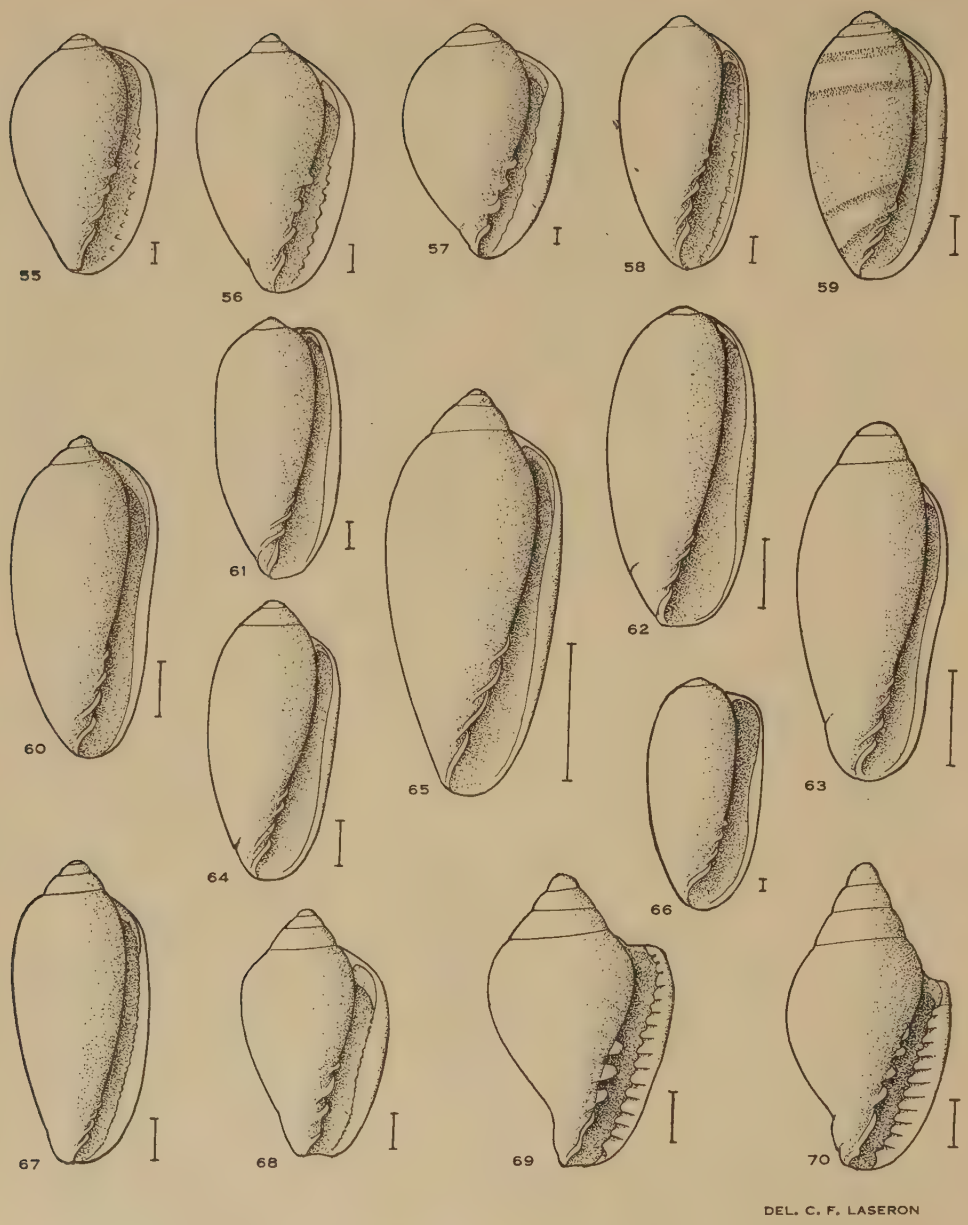


Fig. 37.—*Epiginella ablita*, sp. nov. Holotype. Fig. 38.—*Ovaginella ovulum* (Sowerby). Fig. 39.—*Microginella anxia* (Hedley). Fig. 40.—*M. opima*, sp. nov. Holotype. Fig. 41.—*M. vitrea*, sp. nov. Holotype. Fig. 42.—*Phyloginella simplex*, sp. nov. Holotype. Fig. 43.—*P. pachia* (Watson) (after Watson). Fig. 44.—*P. compressa*, sp. nov. Holotype. Figs. 45–48.—*Euliginella angasi* (Crosse), showing variation. Fig. 49.—*E. melwardi*, sp. nov. Holotype. Figs. 50–51.—*Kogomea striata*, sp. nov. Holotype. Fig. 52.—*Neptoginella fascicula*, sp. nov. Holotype. Fig. 53.—*N. tropica*, sp. nov. Holotype. Fig. 54.—*N. superstes*, sp. nov. Holotype.



Figs. 55 (after Watson), 56.—*Deviginella brachia* (Watson). Fig. 57.—*D. maxilla*, sp. nov. Holotype. Fig. 58.—*D. modulata*, sp. nov. Holotype. Fig. 59.—*Haloginella agata*, sp. nov. Holotype. Fig. 60.—*H. agatha*, sp. nov. Holotype. Fig. 61.—*H. diminuta*, sp. nov. Holotype. Fig. 62.—*H. augerea*, sp. nov. Holotype. Fig. 63.—*H. keppelensis*, sp. nov. Holotype. Fig. 64.—*H. torresina*, sp. nov. Holotype. Fig. 65.—*H. rex*, sp. nov. Holotype. Fig. 66.—*H. infans*, sp. nov. Holotype. Fig. 67.—*Hydroginella dispersa*, sp. nov. Holotype. Fig. 68.—*Austroginella queenslandica*, sp. nov. Holotype. Fig. 69.—*Protoginella lavigata* (Brazier). Fig. 70.—*P. praeterea*, sp. nov. Holotype.

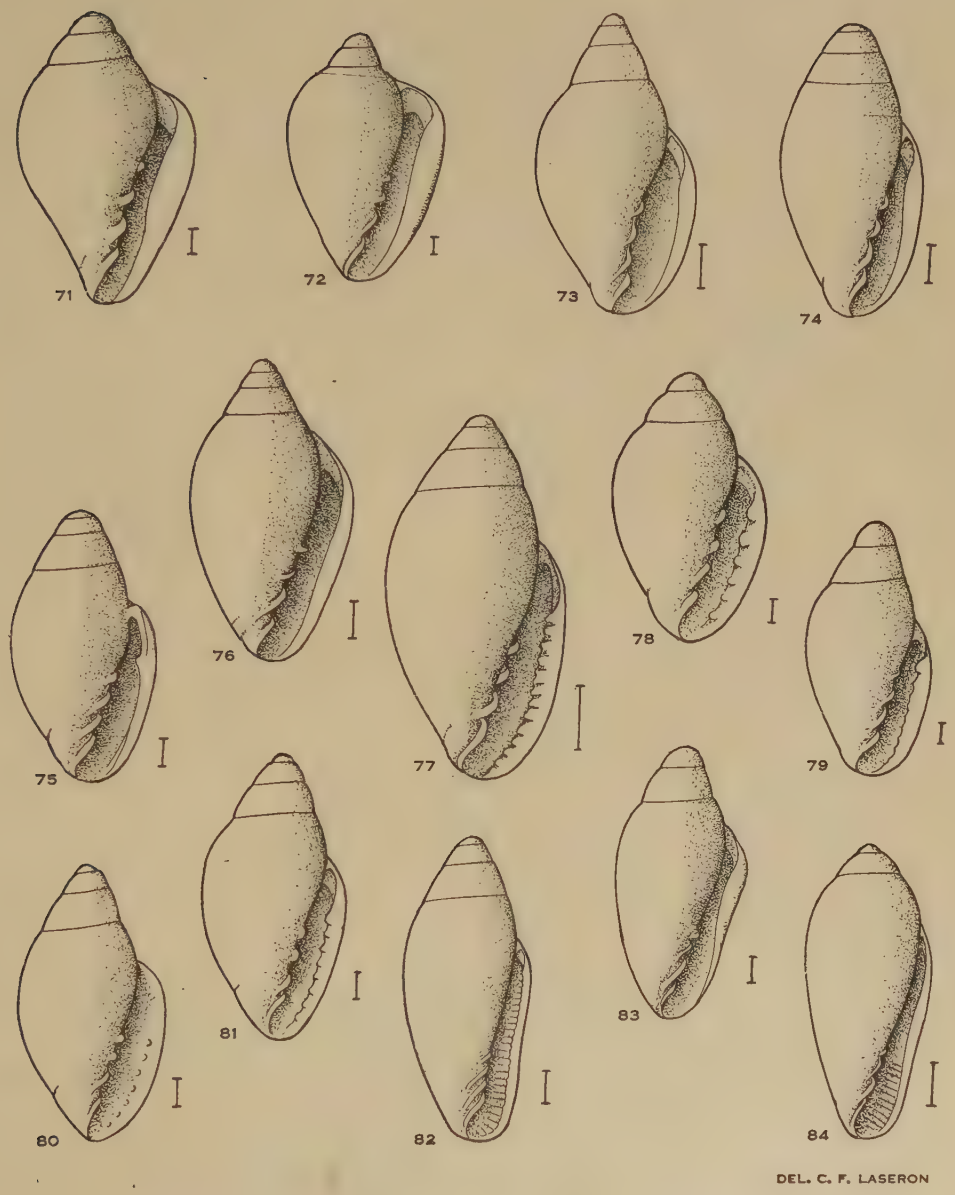


Fig. 71.—*Alaginella albino*, sp. nov. Holotype. Fig. 72.—*A. pygmora*, sp. nov. Holotype. Fig. 73.—*Longinella tropica*, sp. nov. Holotype. Fig. 74.—*L. arvina*, sp. nov. Holotype. Fig. 75.—*L. arvina*, sp. nov. Variation. Fig. 76.—*L. tollere*, sp. nov. Holotype. Fig. 77.—*Volvarinella walkeri* (Smith). Fig. 78.—*V. fortis*, sp. nov. Holotype. Fig. 79.—*V. insecta*, sp. nov. Holotype. Figs. 80 (after Watson), 81.—*V. alta* (Watson). Fig. 82.—*Baroginella infirma*, sp. nov. Holotype. Fig. 83.—*B. volunta*, sp. nov. Holotype. Fig. 84.—*B. attentia*, sp. nov. Holotype.

THE AUSTRALIAN PORTUNIDS (CRUSTACEA; PORTUNIDAE)

I. THE GENUS THALAMITA

By W. Stephenson* and Joy J. Hudson*

[*Manuscript received December* 12, 1956]

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Summary

Twenty-one species are recorded from Australia, including 3 new species and 10 new records. These are described and illustrated, and a key is given for the known Indo–West Pacific species. First pleopods of the males are considered in greater detail than in past works, and a key based on their features is included. The relative breadth of basal antennal joints varies with sizes of specimens, and is of less taxonomic value than had been supposed. For this and other reasons some species have been relegated to the synonymy.

The relationship of *Thalamita* to other genera, and the existence of species groups within the genus, are discussed and brief biogeographical comments are given.

I. Introduction

The portunids are well represented in Australian waters, and indeed throughout the Indian and Pacific Oceans. They are important faunistically in the diversity of different species which are present, ecologically in the variety of niches occupied, and economically in containing sizeable species which are used for human food (*Scylla serrata* (Forskål) and *Neptunus pelagicus* (L.)).

Although there are numerous Australian records these are scattered through the literature, as are specific descriptions. Several of the existing "species" appear to be synonyms, and this together with the inadequacy of many past descriptions has made identifications difficult and questionable.

In the present series of papers consolidation of the literature has been attempted. Descriptions have been amplified in some directions and arranged to facilitate rapid and accurate identification. In particular, adequate illustrations have been attempted. With one exception descriptions have been made *de novo* from specimens in collections

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at Australian institutions, and examinations of these specimens have also added to our knowledge of habitats and distribution.

The present paper is the first of several dealing with the family; others will appear at intervals. The genus *Thalamita* has been selected for priority treatment because: (1) it contains more Australian species than any other genus; (2) it is possibly the most difficult genus in the family; (3) there has been no comprehensive study or revision since Alcock (1899).

The main difficulty within the genus is with juveniles and in avoiding confusion of these with the adults of smaller species. One of the characters used extensively by previous authors was the ratio between the length of the basal antennal joint and width of the orbit. During the present work, in every species for which an extensive size range was available it was noted that the ratio increased with the size of the specimens. Early in the present work four "new species" were isolated, largely on the basis of the above ratio, and these later proved to be juveniles of known species. Several existing species are also considered to be synonyms, because undue stress has been laid upon this feature. These include *T. gardineri* Borradaile, *T. alcocki* de Man, and *T. investigatoris* Alcock, all considered synonymous with *T. picta* and dealt with later.

Although the relative length of the basal antennal joint is not a "good" character, the ornamentation of the joints is extremely "good". They have been described throughout the literature but have rarely been figured. Most of the existent figures are little more than diagrams, and in the present paper photographs or recognizable figures are presented. The latter are free-hand drawings made with the assistance of eyepiece micrometers.

It seems likely that in previous descriptions insufficient allowance has been made for the effects of wear and tear, especially upon the chelipeds. The sharpness of the spines and distinctness of the carinae are greatest in freshly moulted specimens, and decrease with wear. There is also a tendency for cheliped granulation to be more conspicuous in larger specimens. For these reasons, basing specific differences upon surface features of chelipeds requires caution. In the present work several species close to *T. admete* have been fused with it, and the description of *T. picta* has been amplified to include variations in granulation. It is possible that in both these species some of the variations are genetically controlled, but the absence of constant differences on other features suggests that no subspecific status should be given.

On the other hand, in some sections of the genus cheliped ornamentation is highly specific. For example, sharp elongate cheliped spines are a constant feature of *T. prymna*, *T. coeruleipes*, and *T. spinimana*.

The systematic importance of first pleopods in male brachyurans has been stressed by Stephensen (1945) who listed the few species of *Thalamita* for which figures existed. These have been added to by Stephensen (1945) and Edmondson (1954) but are still unknown for many species. Moreover several published figures are barely adequate, few indicate the orientation of the appendages, and there are only fragmentary descriptions. Late in the present work it was realized that the structure of these pleopods, and especially the shape and bristling near their tips,

would allow precise identifications to be made, quite apart from those made on general macroscopic features. Even later it became apparent that appearances altered with the method of preparation. The first preparations were mounted in balsam after treating with caustic potash and staining in fast green. These show the smaller bristles on the proximal part of the appendage particularly clearly but suffer from several drawbacks: bristles tend to be lost during preparation; careful focussing is necessary to resolve confusion between upper bristles and lower ones visible by transparency; and in certain species tips roll over during flattening. This makes it almost impossible to compare structures on the outer and inner sides throughout a series of appendages. The present descriptions stress these inner and outer surfaces, as viewed on an unflattened appendage as from the ventral surface, with abdomen uplifted. The figures are sometimes from permanent preparations and sometimes from temporary mounts in glycerine and alcohol. All are from camera lucida drawings.

II. Description of Genus and Species

Genus THALAMITA Latreille

Thalamita Latreille, 1829, p. 33 (footnote). Milne Edwards, A., 1860, p. 228; 1861, p. 354. Miers, 1886, p. 193. Alcock, 1899, pp. 72–3. Barnard, 1950, p. 171.

Carapace.—Roughly hexagonal, much broader than long (breadth approx. 1·5 times length). Fronto-orbital margin very broad, anterolateral margins normally either subparallel or only slightly divergent posteriorly, posterolateral angles evenly curved. Front cut into 2, 4, or 6 rounded or subquadrate lobes excluding the broad inner orbital lobes. Upper orbital margin with 2 fissures.

Anterolateral teeth.—Typically 5, 4th frequently the smallest, sometimes rudimentary (visible with difficulty), sometimes completely absent. In a small minority of species only 3 teeth present, and in another minority 1st tooth bears a small subsidiary tooth.

Carapace ridges.—The longest, the epibranchials, run between the last anterolateral teeth and are interrupted by the cervical grooves. Anterior to the epibranchials, there are from front to rear: a pair of frontals, normally rounded; a pair of protogastric, broadly separated; and a pair of mesogastric ridges which sometimes join medially. Behind the epibranchials typically no ridges are present, but there may be a centrally placed cardiac, or transverse series of cardiac ridges; outside which there may be either 1 or 2 pairs of mesobranchials.

Basal antennal joint.—Very broad, apical lobe long and in contact for its whole length with the inner orbital tooth, thus completely excluding the rest of the antenna from the orbit. Length of basal antennal joint relative to width of the orbit varies within a species, becoming relatively longer in larger specimens, which makes it of doubtful diagnostic value. Joint variously ornamented with carinae, granules, tubercles, or spines, which are of diagnostic value.

Male abdomen and pleopods.—Third to 5th abdominal segments fused. The shapes of penultimate and ultimate segments are of diagnostic value but difficult to

describe in precise terms, so are excluded from the subsequent descriptions but are figured. Second pair of pleopods bifid; 1st pair tubular and of diagnostic value.

Chelipeds.—Strong, often 1 enlarged. Anterior border of arm typically with 3 stout spines, wrist with long spine on inner margin and 3 smaller spines (often reduced to tubercles) on outer margin. The uppermost and lowermost of these spines generally connected to a carina, as is the innermost spine. On the hand, 4 surfaces are distinguishable, upper, outer, inner, and lower. The upper typically bears on inner side 2 spines lying on a carina, outer is similar with addition of a large proximal spine near the wrist articulation. Outer surface usually bears carinae on the hand, these becoming

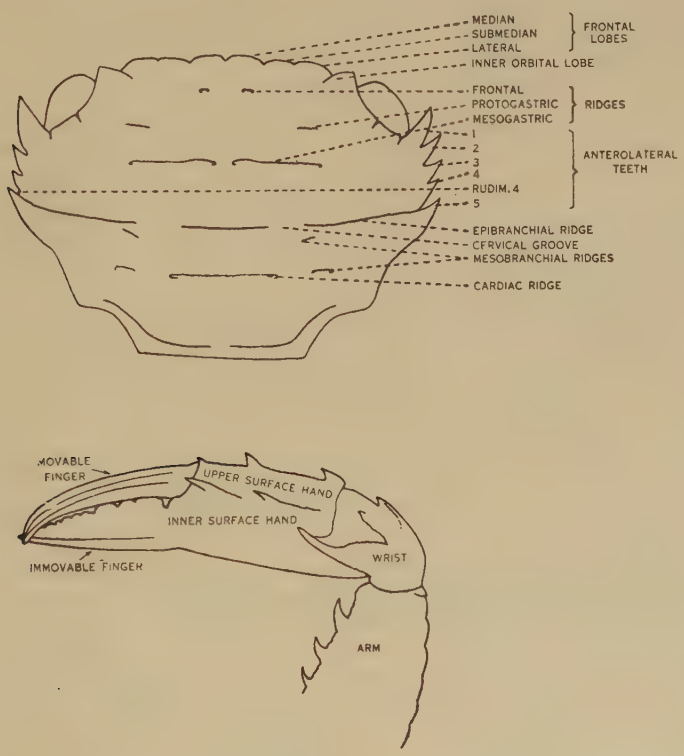

Fig. 1.—Carapace (*above*) and cheliped (*below*) of a generalized *Thalamita*.

more pronounced on the immovable finger. On inner surface, carina sometimes present on the hand, and finger is also grooved. Under surface usually smooth but sometimes bearing squamiform markings. Typically, both movable and immovable fingers bear strong teeth.

Fifth leg.—All segments conspicuously flattened, posterior border of merus with strong spine, and posterior border of propodus generally with row of small spines.

The features of a generalized *Thalamita* are shown in Figure 1, and a discussion of the distinctives of the genus is given later.

KEY TO THE INDO-PACIFIC SPECIES OF THE GENUS THALAMITA, BASED ON GENERAL FEATURES

Paginated references are given only for species not recorded from Australia. Variable species or those obscurely separated by the couplets appear more than once in the keys.

1. Front (excluding inner orbital lobes) normally 6-lobed (abnormal specimens may be 4-lobed) 2
   Front 4-lobed 20
   Front 2-lobed 36

2(1). First anterolateral tooth entire 3
   First anterolateral tooth with tiny subsidiary basal tooth 16

3(2). Fourth anterolateral tooth large (equal to or larger than 5th) 4
   Fourth anterolateral tooth small or absent (smaller than 5th) 7

4(3). Ridge on basal antennal joint with a row of granules 5
   Ridge on basal antennal joint with a row of spines 6

5(4). Inner surface of hand of cheliped with a line of granules (4th anterolateral tooth very slightly smaller than 5th) ..... *T. danae* Stimpson (1858)
   Inner surface of hand of cheliped smooth ..... *T. crenata* (Latreille) (1829)

6(4). Inner margin of upper surface of hand of cheliped typically with 4 spines (rarely 3); carapace relatively broad (breadth/length 1·56 or greater) .. *T. spinimana* Dana (1852*a*)
   Inner margin of upper surface of hand of cheliped with 2 spines; carapace relatively long (breadth/length 1·49 or less) ..... *T. coeruleipes* Jacquinot & Lucas (1853)

7(3). Ridge on basal antennal joint with long spines 8
   Ridge on basal antennal joint with granules, serrations or low teeth 9
   Ridge on basal antennal joint with crest acute and smooth .. *T. picta* Stimpson (1858)
   Ridge on basal antennal joint almost indistinguishable .... *T. imparimana* Alcock (1899, p. 87)

8(7). Two large fused teeth on basal antennal joint (structure of basal antennal joint, and fact that it is shorter than the orbit, may be due to the small size—13 mm—of the holotype) ..... *T. tenuipes* Borradaile (1902, pp. 204–5, Fig. 35)
   Three to 5 teeth on basal antennal joint ..... *T. prymna* (Herbst) (1794)

9(7). Median frontal lobes very broad; submedian and lateral frontal lobes very narrow (original description mentions only lateral lobes but these may have 2 processes) ... . *T. medipacifica* Edmondson (1954) (see *T. dakini* Montgomery (1931))
   Frontal lobes not so arranged 10

10(9). Lateral and submedian frontal lobes barely distinguishable, effectively forming 1 sinuous lobe ..... *T. malaccensis* Gordon (1938, pp. 176–9, Figs. 2, 3)
   Lateral and submedian frontal lobes distinguishable 11

11(10). Ridges present on carapace posterior to epibranchial ridges 12
   Ridges not present on carapace posterior to epibranchial ridges 13

12(11). Median and submedian frontal lobes almost combined into 2 broad flat lobes .... *T. wakensis* Edmondson (1925, p. 38)
   Median and submedian frontal lobes rounded and clearly separated by deep notches ..... *T. picta* Stimpson (1858)

13(11). Four anterolateral teeth (3rd very small) ..... *T. bandusia* Nobili (1905, p. 402)
   Five anterolateral teeth 14

14(13). Species small, maturing at 9 mm; basal antennal joint only half width of orbit in 9 mm specimen ..... *T. kukenthali* de Man (1902, pp. 650–1)
   Species large; smallest mature specimen *c.* 40 mm. Basal antennal joint even in smallest specimen (6 mm) two-thirds diameter of orbit, typically very much more than orbit) .. 15

15(14). Fourth anterolateral tooth very slightly smaller than 5th ..... *T. danae* Stimpson (1858)
Fourth anterolateral tooth very much smaller than 5th ..... *T. stimpsoni* A. Milne Edwards (1861)

16(2). Median frontal lobes much narrower than submedians. *T. macropus* Montgomery (1931)
Median frontal lobes almost as broad as submedians 17

17(16). Variable number of spines on posterior border of propodus of 5th leg 18
No spines on posterior border of propodus of 5th leg 19

18(17). Fourth anterolateral tooth rudimentary .... *T. macrospinifera* Rathbun (1911, p. 209)
Fourth tooth of normal size ..... *T. spinifera* Borradaile (1902, p. 203)

19(17). Fifth anterolateral tooth much smaller than 3rd ..... *T. exestastica* Alcock (1899, pp. 86–7)
Fifth anterolateral tooth nearly as large as 3rd and projects somewhat more than the rest (median frontal lobes distinctly narrower than submedians) ..... *T. macrodonta* Borradaile (1902, p. 203)

20(1). Median frontal lobes narrower than laterals 21
Median frontal lobes much broader than laterals 26

21(20). Front perfectly straight 22
Front sinuous, median frontal lobes more prominent than laterals 23

22(21). Carapace barely more than $1\frac{1}{2}$ times as broad as long; anterolateral margins pointing directly forwards ..... *T. intermedia* Miers (1886)
Carapace broad, $1\frac{3}{4}$ times as broad as long; anterolateral margins markedly oblique .... *T. annulipes*, sp. nov.

23(21). Median frontal lobes moderately prominent; 5 anterolateral teeth 24
Median frontal lobes conspicuously prominent; 4 anterolateral teeth of which 3rd is smallest ..... *T. hanseni* Alcock (1899, pp. 88–9)

24(23). Fourth anterolateral tooth much smaller than 5th (merus of 5th leg bears a spine on posterior border) 25
Fourth anterolateral tooth not much smaller than 5th ..... *T. kagosimensis* Sakai (1939, pp. 419–20, Fig. 14)

25(24). Posterior border of propodus of 5th leg smooth ..... *T. sexlobata* Miers (1886)
Posterior border of propodus of 5th leg bearing a series of minute denticles ..... *T. malaccensis* Gordon (1938, pp. 176–9, Figs. 2, 3)

26(20). Four anterolateral teeth 27
Five anterolateral teeth 30

27(26). Third anterolateral tooth as large as 2nd 28
Third anterolateral tooth rudimentary 29

28(27). Five spines on hand of cheliped, including that at wrist articulation ..... *T. cooperi* Borradaile (1902)
Three spines on hand of cheliped ..... *T. invicta* Thallwitz (1891, p. 46, Fig. 11) = *T. de mani* Nobili (1905, p. 402)

29(27). Hand of cheliped bearing 5 blunt spines and 1 ridge ..... *T. inhacae* Barnard (1950)
Hand of cheliped bearing 3 spines and 3 carinae .. *T. bouvieri* Nobili (1906*b*, p. 262)

30(26). Fourth anterolateral tooth as large as 5th ..... *T. crenata* (Latreille) (1829) (unusual specimens)
Fourth anterolateral tooth smaller than 5th 31

31(30). Outer surface of hand of cheliped nearly smooth (fingers shorter than palm) ..... *T. taprobanica* Alcock (1899, p. 91)
Outer surface of hand of cheliped with granular costae 32

32(30). Median frontal lobes resolvable into 2 broad overlapping lobes ..... *T. wakensis* Edmondson (1925, p. 38)
Median frontal lobes normal not as above 33

33(32). Basal antennal joint with granular ridge 34
Basal antennal joint with a low microscopically granular crest (4th anterolateral tooth very small or rudimentary) 35
Crest on basal joint with row of 3 large spines ..... *T. quadrilobata* Miers (1884)

34(33). Fourth anterolateral tooth rudimentary ..... *T. seurati* Nobili (1906*b*, p. 262)
Fourth anterolateral tooth small, but far from rudimentary ..... *T. dakini* Montgomery (1931) and *T. medipacifica* Edmondson (1954)

35(33). Five spines on upper surface of hand of cheliped; sternum and abdomen of ♂ glabrous and pitted; 1st pleopod of ♂ stout ..... *T. wood-masoni* Alcock (1899, pp. 90–1)
Six spines on upper surface of hand of cheliped; sternum and abdomen of ♂ with setose grooves; 1st pleopod of ♂ slender distally ..... *T. delagoae* Barnard (1950, pp. 178–9, Fig. 33*h*, *i*)

36(1). Inner orbital lobes strongly arched and much narrower than frontal lobes 37
Inner orbital lobes straight or little arched and not much narrower than frontal lobes. 47

37(36). Median frontal notch clearly marked 38
Median frontal indistinct (outer surface of hand of cheliped usually smooth or very indistinctly costate except for costae running to the immovable finger) 44

38(37). Surface of sternum and abdomen with numerous transverse sculptures ..... *T. oculea* Alcock (1899, p. 91)
Surface of sternum and abdomen generally smooth 39

39(38). Outer surface of hand of cheliped very indistinctly costate ..... *T. bilobata* de Man (1926, pp. 199–204, Plate 1, Figs. 1–1*d*)
Outer surface of hand of cheliped distinctly costate 40

40(39). Five anterolateral teeth 41
Four anterolateral teeth 43

41(40). Frontal lobes not markedly prominent 42
Frontal lobes project markedly forwards ..... *T. gracilipes* (A. Milne Edwards) (1873, pp. 169–71, Plate 4, Fig. 3*a–d*); and *T. anomala*, nom. nov. for *Thalamonyx danae* A. Milne Edwards (1869, p. 153, Plates VII, VIII)

42(41). Conspicuous squamiform markings on under surface of hand in all but very small specimens ..... *T. sima* H. Milne Edwards (1834)
No squamiform markings on under surface of hand ..... *T. iranica* Stephensen (1945, pp. 128–33, Figs. 29, 30)

43(40). Crest on basal antennal joint bearing 4 blunt teeth ..... *T. pilumnoides* Borradaile (1902, p. 207, Fig. 38)
Crest on basal antennal joint very acute and microscopically denticulate ..... *T. minuscula* Nobili (1906*b*, p. 262)

44(36). Anterolateral teeth acute 45
Anterolateral teeth square-cut 46

45(44). Ventral inner orbital lobe only slightly prominent ..... *T. poissoni* (Audouin & Savigny) (1825) (see Sakai 1939, pp. 423–5, Plate LXXXV, Fig. 2)
Ventral inner orbital lobe very prominent ..... *T. iranica* Stephensen (1945, pp. 128–33, Figs. 29, 30)

46(44). Distinct branchial ridges on carapace ..... *T. chaptali* (Audouin & Savigny) (1825)
No branchial ridges on carapace .. *T. parvidens* Rathbun (1907, p. 62, Plate 5, Fig. 2)

47(36). Crest on basal antennal joint smooth or microscopically granular 48
Crest on basal antennal joint granular or dentate 49
Crest on basal antennal joint spinous ..... *T. quadrilobata* Miers (1884)

48(47). Progastric region of carapace either smooth or with rounded granular elevations, but without ridge ..... *T. integra* Dana (1852*b*)
Progastric region of carapace with short granulated ridge ..... *T. integra africana* Miers (1881, p. 218)

49(47). Space between the 2 lowermost ridges on outer surface of hand of cheliped smooth or only very sparsely granular 50
Space between the 2 lowermost ridges on outer surface of hand of cheliped granular .. 52

50(49). Anterolateral teeth typically 4, sometimes 3 ..... *T. spiceri* Edmondson (1954, pp. 258–60, Fig. 33*a–e*) (doubtfully separate from *T. admete*)
Anterolateral teeth typically 5, sometimes 4 51

51(50). No minute lateral frontal lobes ..... *T. admete* (Herbst)(1803)
Minute lateral frontal lobes ..... *T. medipacifica* Edmondson (1954) (see *T. dakini* Montgomery)

52(49). Fourth anterolateral tooth small, but not rudimentary (under surface of hand of cheliped granular) ..... *T. granosimana* Borradaile (1902, p. 202)
Fourth anterolateral tooth rudimentary 53

53(52). Fifth anterolateral tooth long, produced as long as the 3rd tooth ..... *T. margaritimana* Rathbun (1911, p. 202, Plate 15, Fig. 12)
Fifth anterolateral tooth short, not produced as long as the 3rd tooth ..... *T. auauensis* Rathbun (1906, p. 874, Plate XII, Fig. 1)

Key to the Indo-Pacific Species of the Genus Thalamita, Based on First Male Pleopods

The restricted nature of the key is due to the fact that the structure of the pleopods is undescribed for many species. Only when the pleopods are not figured in the present work is a reference given to the literature. The key deals only with structures at and near the tips of the appendages. Orientations are given from an unflattened appendage viewed as from the ventral surface, with abdominal flap uplifted.

1. Tip enlarged (outline looks like human leg and foot) 2
Tip sharply turned, sometimes turned over backwards 5
Tip rounded and slightly bulbous ..... *T. trilineata* (see Fig. 3*E*)
Tip abruptly and slightly obliquely truncated 6
Tip gradually tapering 8

2(1). Bristles on outer side only ..... *T. sexlobata* (see Fig. 3*B*) = *T. poissonii* Sakai (1939, Fig. 17, non auct.)
Bristles on both inner and outer sides 3

3(2). Tip curvedly flaring, reminiscent of lily flower ..... *T. sima* (see Fig. 3*C*)
Tip truncated and square-cut 4

4(3). Inner bristles short and stout ..... *T. picta* (see Fig. 3*A*)
Inner bristles long and hair-like ..... *T. wakensis* (Edmondson 1954, Fig. 36*d*)

5(1). Longest outer bristles *c.* 1½ times diameter of appendage opposite them, *c.* 9 outer bristles and 5 inner ..... *T. poissoni* (Stephensen 1945, Fig. 31*F*)
Longest outer bristles just longer than diameter of appendage, *c.* 12 outer bristles and 3 inner ..... *T. chaptali* (see Fig. 3*F*)
Longest outer bristles just longer than diameter of appendage, 3 outer bristles and few inner bristles, possibly 1-3 ..... *T. delagoae* Barnard (1950, Fig. 33*i*)
Longest outer bristles just shorter than diameter of appendage, *c.* 3 outer bristles and *c.* 10 inner bristles ..... *T. parvidens* Sakai (1939, Fig. 19*b*)

6(1). Bristles all long and hair-like; outer bristles numerous 7
Bristles all short; few outer bristles ..... *T. wood-masoni* (Barnard 1950, Fig. 33*f*)
Inner bristles short; outer bristles long; moderate number of outer bristles ..... *T. intermedia* (see Fig. 4*C*)

7(6). All outer bristles thin and hair-like ..... *T. annulipes* (see Fig. 3*D*)
Some outer bristles near the tip robust ..... *T. iranica* (Stephensen 1945, Fig. 29*E*)

8(1). Bristles very long, stout, and almost at right angles to appendage 9
Bristles not as above 11

9(8). Four or 5 very stout bristles on one side (? outer) of appendage and none on the other ..... *T. medipacifica* (Edmondson 1954, Fig. 34*g*, *h*)
Four or 5 very stout bristles on both sides of appendage ..... *T. auauensis* (Edmondson 1954, Fig. 32*c*, *d*)
Four or 5 very stout bristles on inner side, more than 10 on outer ..... *T. quadrilobata* (see Fig. 3*G*)
Eight or more very stout bristles on inner side; more than 10 on outer 10

10(9). Both very stout and normal bristles on inner side ..... *T. admete* (see Fig. 3*I*)
Only very stout bristles on inner side ..... *T. integra* (see Fig. 3*H*)

11(8). Outer bristles almost at right angles to appendage 12
Outer bristles pointing obliquely distally 13

12(11). About 18 outer bristles ..... *T. spinifera* (Edmondson 1954, Fig. 41*d*)
About 36 outer bristles ..... *T. macropus* (see Fig. 3*J*)

13(11). Inner surface with bristles almost to tip 14
Inner surface with considerable bare area behind tip 15

14(13). Inner bristles very short and stout (wedge-shaped) ..... *T. inhacae* (see Fig. 3*L*)
Inner bristles normal ..... *T. squamosa* (see Fig. 3*K*)

15(13). Outer bristles very numerous, more than 30 ..... *T. spinimana* (see Fig. 3*O*)
Outer bristles numerous, *c.* 20 ..... *T. stimpsoni* (see Fig. 3*M*)
Outer bristles of moderate number, less than 15 16

16(15). Outer side with large tubercle-like spines near tip 17
Outer side without large tubercle-like spines near tip 18

17(16). Two tubercle-like spines, long bare terminal area ..... *T. danae* (see Fig. 3*N*)
Three tubercle-like spines, short bare terminal area ..... *T. coeruleipes* (see Fig. 3*P*)

18(16). Outer bristles closely packed ..... *T. crenata* (see Fig. 3*Q*)
Outer bristles widely spaced ..... *T. prymna* (see Fig. 3*R*)

Specific Descriptions

These follow, in alphabetical order. The synonymy is normally restricted to those papers detailing structural features and excludes merely those recording occurrences. The sections on "Recorded habitats" are based upon records accompanying the specimens examined, which represent the total collections in Australian institutions at January 1, 1955. If characters of a species agree with the general pattern as given in the generic description, these are not repeated.

Thalamita admete (Herbst)

Figs. 2*I*, 3*I*; Plate 1, Fig. 1; Plates 7*A*, 10*A*

Cancer admete Herbst, 1803, pp. 40–1, pl. LVII, fig. 1.

Thalamita admete Latreille, 1829, p. 33 (fide Miers 1886). Milne Edwards, A., 1861, pp. 356–7. Miers, 1884, p. 230. Borradaile, 1900, p. 579. Calman, 1900, p. 23. Lenz, 1905,

Fig. 2.—First male pleopods, flattened preparations, with outer surface on right. Scale lines, 2 mm. *A*, *T. picta*; *B*, *T. sexlobata*; *C*, *T. sima*; *D*, *T. annulipes*; *E*, *T. trilineata*; *F*, *T. chaptali*; *G*, *T. quadrilobata*; *H*, *T. integra*; *I*, *T. admete*; *J*, *T. macropus*; *K*, *T. squamosa*; *L*, *T. inhacae*; *M*, *T. stimpsoni*; *N*, *T. danae*; *O*, *T. spinimana*; *P*, *T. coeruleipes*; *Q*, *T. crenata*; *R*, *T. prymna*. The arrangement follows the second key, with the initial grouping therein as follows: *A–C*; *F*; *E*; *D*; *G–R*; and second main separations between *G–I*, *J–L*, and *M–R* respectively.

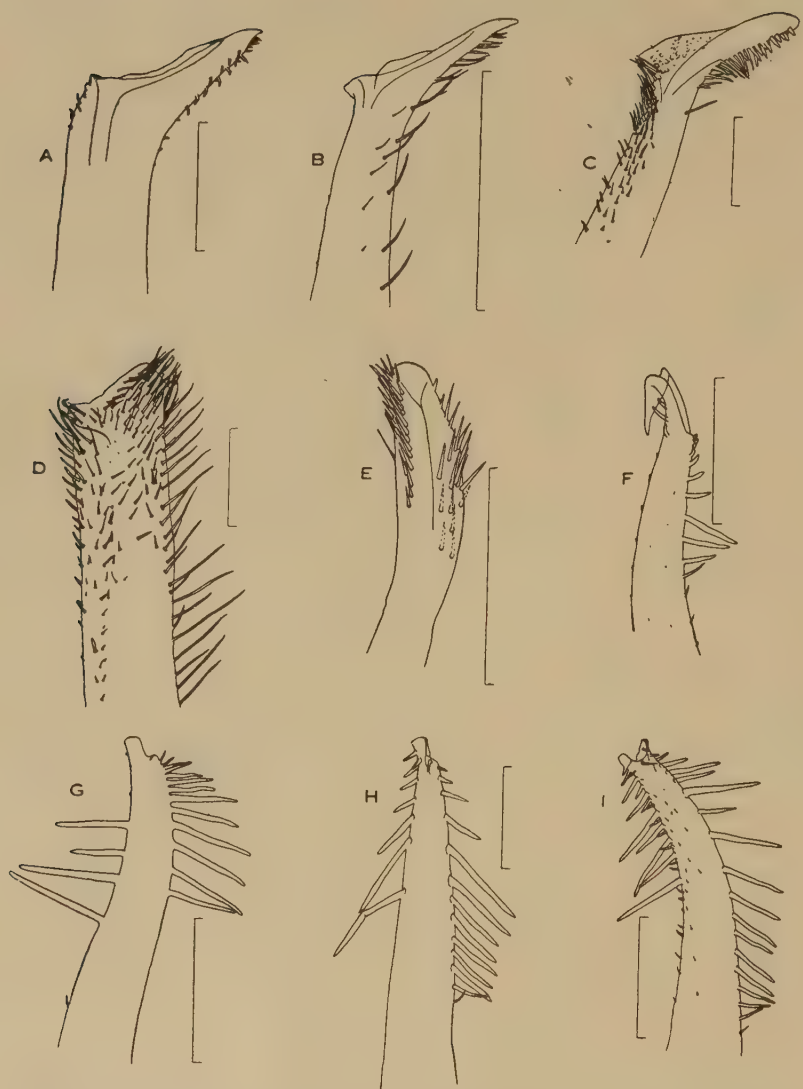

Fig. 3.—Tips of first male pleopods, unless otherwise stated, with outer surface on right. Scale lines, 0·5 mm. Arrangement follows second key as in Fig. 2. *A*, *T. picta*; *B*, *T. sexlobata*; *C*, *T. sima* (bristles of undersurface as seen by transparency are dotted); *D*, *T. annulipes*; *E*, *T. trilineata*, drawn from right pleopod, hence with outer surface on left (dots indicate bristles presumed to be present of which only the sockets were visible); *F*, *T. chaptali* (dots indicate bristles presumed to be present of which only the sockets were visible); *G*, *T. quadrilobata*; *H*, *T. integra*, proximal bristles on inner surface bent in preparation; *I*, *T. admete*.

Fig. 3.—Tips of first male pleopods, unless otherwise stated with outer surface on right. Scale lines, 0·5 mm. Arrangement follows second key as in Fig. 2. *J*, *T. macropus*; *K*, *T. squamosa*; *L*, *T. inhacae*; *M*, *T. stimpsoni*; *N*, *T. danae* (N_1 is unflattened and correctly orientated; N_2 is from a flattened preparation with the tip rolled over); *O*, *T. spinimana*, right pleopod with outer surface on left; *P*, *T. coeruleipes*, right pleopod with outer surface on left; *Q*, *T. crenata* (Q_1 is unflattened and correctly orientated; Q_2 is from a flattened preparation with the tip rolled over); *R*, *T. prymna*.

p. 362. Rathbun, 1911, p. 208. Edmondson, 1923, p. 1550; 1925, p. 37 ; 1954, pp. 255–6, figs. 30*a*, *b*, 31*a–e*. Sakai, 1939, pp. 414, 421–2, pl. LXXXV, fig. 1. Ward, 1942, p. 80. Barnard, 1950, p. 176, fig. 33*c*.

Thalamita savignyi Milne Edwards, A., 1861, pp. 357–8, 367. Ortmann, 1894, p. 46.

Thalamita admeta Alcock, 1899, pp. 82–4 (lit. and synon.).

Thalamita admete var. *edwardsi* Borradaile, 1900, p. 579.

Thalamita admeta var. *A admeta* Borradaile, 1902, pp. 202–3.

Thalamita admeta var. *B edwardsi* Borradaile, 1902, pp. 202–3.

Thalamita admeta var. *C savignyi* Borradaile, 1902, pp. 202–3.

Thalamita edwardsi Rathbun, 1906, p. 874. Edmondson, 1925, p. 37; 1954, pp. 254–5, figs. 28*b*, 29*a–d*.

Thalamita admeta var. *savignyi* Nobili, 1906*a*, pp. 202, 206–8.

Thalamita admete var. *savignyi* Laurie, 1915, pp. 440–1.

?*Thalamita spiceri* Edmondson, 1954, pp. 258–60, fig. 33*a–e*.

Material Examined

85 ♂♂ (9–37 mm); 67 ♀♀ (8–29 mm). Smallest ovigerous ♀ 20 mm; ovigerous ♀♀ from months Jan., April–Oct.

QUEENSLAND: Torres Str. (Moa I., Murray I.); Fly Pt. near Albany Pass; Low Isles; Turtle Reef; Phantom I.; Darnley I.; Holbourne I. (Port Denison); Frankland Grp.; Hamilton I.; Lindeman I.; Hayman I.; Hope I.; C. Upstart; S. Yeppoon; Curtis I.; Rat I.; Capricorn Grp. (Mast Head I., Heron I., North West I., One Tree I.); Bargara; Caloundra Hds.; Moreton Bay (Peel I., Dunwich, Bird I.). NEW SOUTH WALES: Yamba; Stockton Bight; Collaroy; Port Jackson; Broken Bay; Shellharbour. LORD HOWE I. WESTERN AUSTRALIA: Gantheaume Pt.; C. Leveque. NORTHERN TERRITORY: C. Wessel.

Recorded habitats.—Intertidal to 7 fm; both mainland coast and coral reef areas, under stones both large and small, and amongst mussel clumps.

Material illustrated.—Carapace, basal antennal joint, and male abdomen: ♂ 24 mm, S. Yeppoon, near Rockhampton, Qld., 15.i. 53, W. Stephenson (under stone, L.W.S.) (Zool. Dept., Univ. Qld.). Male pleopod: ♂ 25 mm, Low Isles (W. of Old Tripneustes Spit), 13.viii.54, W. Stephenson (Zool. Dept., Univ. Qld.).

Description

Front.—Two broad lobes, separated by distinct notch, with square-cut or slightly concave profile. Inner orbital lobes broad (*c.* $\frac{9}{10}$ width of frontal lobes) and little arched.

Anterolateral teeth.—Four large subequal teeth, 1st the broadest, last the most prominent; a 5th tooth corresponding to 4th of those normally present may be entirely absent, represented by a rudiment, or may be about half the size of the other teeth.

Carapace.—Three normal pairs of gastric ridges present, also epibranchial interrupted by cervical groove and medially; median cardiac and mesobranchial ridges present but more rounded and less obvious. (In 1 specimen, median cardiac and mesobranchial ridges not detectable.) Apart from ridges, entire surfaces of carapace, in recently moulted specimens, covered with fine hairs, removal of which reveals minute granulations.

Basal antennal joint.— Bearing an acute ridge whose edge is formed of 7–12 fused tubercles. Ratio between breadth of this joint and major diameter of orbit ranges from *c.* 1.2 (specimens 12 mm broad) to 1.7 (specimens 24 mm broad).

Chelipeds.—One larger and more massive than the other, sometimes the differences obvious and sometimes not, sometimes right cheliped larger and sometimes left. Anterior border of arm and wrist normal, with upper wrist spines often reduced to tubercles, and with the inner and outer terminating distinct granular crests. Upper surface of hand in a minority of specimens with 5 spines, with 3 on inner and 2 on outer side. (In 1 ♂, Dunwich, 4.vii.51, a small additional spine, lying between the anterior and posterior outer spines.) Generally anterior spine of inner side unrecognizable, and also anterior spine of outer side reduced to a tubercle. Hindermost spines of both inner and outer sides are terminations of granular carinae. In recently moulted specimens, upper surface of hands between spines bears small granules and fine hairs. Outer surface of chelipeds may have only 1 distinct carina, running over lower surface to end of immovable finger. On middle of outer surface there may be only a trace of a rounded carina at distal end, or a just recognizable carina running over entire surface, or a sharp and distinct carina. On upper side of outer surface there may be only an indistinct proximal row of granules or a continuous and heavily beaded ridge. Carination of larger chelipeds always less obvious than in smaller. Inner and lower surfaces of chelipeds smooth and without traces of carinae. Fingers short and stumpy.

Fifth leg.—Merus moderately long, 2–2¼ times as long as broad, and smooth posteriorly, except for usual spine; posterior border of propodus conspicuously spinous, with 5–8 large and 1–2 small spines.

First male pleopod.—Short, stout, slightly curved, tip very slightly flared. Beyond basal lobes, bare on both surfaces about half way up, followed by very sparsely arranged short, stout, curved hairs (only visible in stained preparation). Middle of upper surface also bearing short, stout hairs directed forwards (only visible in stained preparation). *Terminal bristles on inner surface.*—Beginning well back as a series of short, curved bristles proximally arranged in pairs, then continuing as single bristles to tip, *c.* 14 in the series. A 2nd series of 4–8 very long stout bristles directed slightly backwards, increasing in size proximally. *Terminal bristles on outer surface.*—Eighteen to 20 long, stout, backwardly directed bristles, the 2 longest bristles separated by a shorter one and situated about one-third of the way from the tip. There is a general decline in size proximally and the last 3 bristles are inclined progressively, distally. These outer bristles extend for about one-quarter to one-third of the way back along the pleopod. Upper surface bears approximately 20 short bristles anteriorly directed.

Colour.—After a year in alcohol, general surface profusely mottled with reddish brown. Anterolateral teeth and spines of chelipeds tipped with dark brown, fading at extremities. Outer surface of hand of cheliped has distinct red spots, also present on upper side of inner surface. Distal half of fingers dark brown fading at tips. Proximal to this, a distinct brown band runs across the movable finger, midway between its insertion and beginning of brown area. Colour alive varying from light fawn to dark brown (depending upon environment) and with mottling.

Comments

The fact that this is an extremely variable species is apparent from the synonymy. The consensus of opinion is that A. Milne Edwards's *Thalamita savignyi* is merely a variant, and the only dubious point appears to be the status of Borradaile's

"var. *edwardsi*", which is typified by the carination and granulation of the outer surface of the hand of the chelipeds. The existence of gradations between smoothness and carination, together with the absence of any correlated characters which would serve for distinction, suggests that this "variety" should not be retained. The variation in size of the 4th anterolateral tooth will also be noted, and in Herbst's figure and description this tooth is quite reasonably large.

Distribution

Published and present records within Australia are from Queensland (Miers 1884; Calman 1900; Grant and McCulloch 1906–7; McNeill 1926; Stephenson *et al.* 1931), New South Wales (Miers 1884; Stead 1898; Ward 1937), and Lord Howe I. (Rathbun 1906; Edmondson 1925; McNeill 1934–7); now also from Northern Territory and Western Australia. Most southerly record on east coast is from 27° S., 114° E., and on west coast from 34° S., 151° E.

In the west, from the Red Sea (Laurie 1915) to Durban (Barnard 1950) and Mauritius (Ward 1942); throughout the Indian Ocean; in the east, from south Japan (Sakai 1939) to Hawaii (Edmondson 1923, 1925) and Fiji (Miers 1886).

Thalamita annulipes, sp. nov.

Figs. 2*D*, 3*D*; Plate 1, Fig. 2; Plates 7*B*, 9*A*

Material Examined

WESTERN AUSTRALIA: Holotype ♂ 33 mm (*Sacculina*-infected), between tide marks, Gantheaume Pt., Broome, Sept. 1929, A. A. Livingstone (Aust. Mus.).

Material illustrated.—As above.

Description

Front.—Four-lobed, medians slightly more than half breadth of laterals, projecting slightly beyond them. Both medians and laterals have flat anterior surfaces, giving whole front a flat appearance resembling that of *T. intermedia*. Inner orbital lobes barely arched and slightly longer than lateral frontal lobes.

Anterolateral teeth.—Five, 1st large and stout, 2nd large and sharp, 3rd slightly smaller, 4th small and acute, 5th longer and acute.

Carapace.—Very broad, breadth 1·75 times length. Anterolateral borders distinctly inclined as in *Thalamonyx* (Milne Edwards 1873, p. 168; Alcock 1899, p. 71). Usual 3 gastric ridges present, also epibranchials, but these last not continued between cervical grooves. No cardiac ridge, but small posterior mesobranchials. Carapace densely covered with extremely short hairs, giving a matt appearance.

Basal antennal joint.—Distinctly longer (1·3 times) than orbit bearing low ridge with larger rounded granules, regularly spaced some distance apart.

Chelipeds.—Right much more massive than left, both with conspicuous squamiform tubercles on carinae and under surfaces. Anterior borders of arm bear 3 spines (right) or 2 (left). Wrist spinulation normal, hand spines normal and well developed apart from anterior distal spine of right hand. Three well-marked carinae on outer side of hands, 1 on centre of inner surface.

Fifth leg.—Merus just over twice as long as broad, usual spine on posterior border; upper posterior distal margin spiniform; posterior margin of propodus with 7–8 well-developed spines.

First male pleopod.—Short, very stout, practically straight, tip obliquely and abruptly terminating. Outer surface with long hairs more than half length of appendage. *Terminal bristles.*—Continuous from inner to outer surfaces. Inner surface with *c.* 25 bristles, arranged in indistinct rows, pointing distally, increasing in length towards tip. Outer surface with *c.* 60 elongate hair-like bristles visible in profile view, distal ones the shortest and thickest, proximal ones the thinnest.

Colour.—Biscuit conspicuously marked with purple-brown as follows: outlining mesogastric ridges, spots on mesobranchial region, tips of fingers, and spines of chelipeds, and as broad conspicuous bands on the walking legs. Two bands cross each dactylus, propodus, and merus; a single band on each carpus.

Comments

While the facies of this specimen may have been affected by *Sacculina* infection it seems distinctive enough to justify the erection of a new species. The specific epithet refers to the banded walking legs. The inclination of the anterolateral borders would place this species in the genus *Thalamonyx* A. Milne Edwards, provided the generic definition was modified to include species with 4-lobed fronts. As de Man has already pointed out, there is little to justify separation of *Thalamonyx* from *Thalamita.* For example, certain species which definitely belong to *Thalamita* (e.g. *T. sima*) have distinctly inclined anterolateral borders.

It seems likely that *Thalamonyx* should disappear into the synonymy of *Thalamita*, in which case *Thalamonyx danae* will need a new specific epithet (see p. 361). The present species is close to *T. intermedia*, especially as regards the male pleopod.

Thalamita chaptali (Audouin & Savigny)

Figs. 2*F*, 3*F*; Plate 1, Fig. 3; Plates 7*C*, 10*B*

Portunus chaptali Audouin and Savigny, 1825, pl. iv, fig. 1.
Thalamita chaptali Milne Edwards, A., 1861, pp. 360, 367. Alcock, 1899, pp. 80–1 (lit. and synon.). Nobili, 1906*a*, pp. 202, 205. Rathbun, 1910*b*, p. 365, fig. 44.

Material Examined

26 ♂♂ (8–26 mm); 31 ♀♀ (7–21 mm). Smallest ovigerous ♀, approx. 10 mm; *Sacculina* infection 3 per cent.

QUEENSLAND: C. York, Murray I., North Direction I., Low Isles, Lady Musgrave I. LORD HOWE I.

Recorded habitats.—All dredged from near coral structures, at 4–20 fm.

Material illustrated.—Carapace, basal antennal joints, male abdomen, and male pleopod: ♂ 16 mm, C. York, Coll. R.B. (Qld. Mus.).

Description

Front.—Bilobed, forming broad curved arch with small, barely distinct median notch. Inner orbital lobes arched and much narrower than frontal lobes.

Anterolateral teeth.—Five; 1st 3 large and square-cut, 4th smallest, 5th slightly larger than 4th and sharpest of the 5.

Carapace.—Sparsely beset with short, stout hairs. Frontal ridges represented by rounded elevations; protogastrics unrecognizable; mesogastrics strongly developed, slightly undulating, and not obviously broken in the mid line; epibranchial strongly curved, broadly interrupted by cervical grooves and also medially; lateral cardiac ridges short but distinct. Median cardiac ridge not distinct, but just in front of its expected position a deep transverse groove.

Basal antennal joint.—Much shorter than orbit, with short, acute, minutely granular crest.

Chelipeds.—Right cheliped much more massive than left (only 1 specimen examined was complete with both chelipeds). Three teeth on anterior border of arm, ranging from sharp to blunt; surface proximal to 1st tooth, and also posterior margin, granular. Upper surface of wrist with obsolescent spines and faint carinae on outer margin. Hands slightly swollen with 2 carinae on upper surface, each with obsolescent spines in middle of their lengths and even less distinct spines at distal ends. Outer surface of hand sometimes without detectable carina and sometimes with just detectable carina. Apart from small granules on upper surface of hand, remainder smooth or microscopically granular. Fingers short and blunt in large cheliped of ♂, otherwise narrow and elongate.

Fifth leg.—Merus elongate, *c.* 2·6 times as long as broad, with usual spine, and also with occasional plumose hairs concentrated into tufts at distal end. Similar hairs regularly arranged on the remaining segments. Propodus without spines.

First male pleopod.—Smoothly curving, somewhat elongate, with pointed, recurved, slightly flared tip. General surface beyond basal lobes apparently smooth up to region of terminal bristles but actually bearing small distally pointing spinules, whose position becomes obvious on outer face in distal half of appendage. *Terminal bristles on inner side.*—Two obvious bristles, lying somewhat back from tip; short, curved, pointing distally, the distal the shorter; an inconspicuous short 3rd recumbent bristle. *Terminal bristles on outer side.*—Proximally 3 distally pointing hairs, followed by a series of stout bristles resolvable into 4 or 5 proximal ones, followed by 4 distal ones. The former include the 2 longest and stoutest bristles which point proximally, while the latter are short and hooked, and point distally. In addition, near tip, usually (in 2/3 cases) 2 additional stout hooked bristles lying below lateral series.

Comments

The frontal notch varies from being virtually indistinguishable to small but distinct. The specimens differ from Alcock's (1899) description in possessing 3 teeth on the anterior border of the arm and also in that the granulation of the upper surface of the chelipeds is not at all obvious in most specimens. The shape of the front, and that of the anterolateral teeth, are diagnostic.

Distribution

Red Sea (A. Milne Edwards 1861); Ceylon (Laurie 1906); India (Alcock 1899); Gulf of Siam (Rathbun 1910*b*); now Australia.

THALAMITA COERULEIPES Jacquinot & Lucas

Figs. 2*P*, 3*P*; Plate 2, Fig. 1; Plates 7*D*, 9*B*

Thalamita coeruleipes Jacquinot and Lucas, 1853, pp. 53–4, pl. 5, fig. 6. Milne Edwards, A., 1861, pp. 363–4, 367. Ortmann, 1893, p. 85. De Man, 1895, pp. 568–9; 1896, fig. 12. Rathbun, 1906, p. 873. Mijake, 1939, pp. 171–2, pl. XII (1), fig. 1, text fig. 1. Edmondson, 1954, pp. 265–7, figs. 38*a–f*, 39*a*.

Material Examined

11 ♂♂ (15–58 mm); 8 ♀♀ (32–50 mm). Smallest ovigerous ♀ 49 mm; ovigerous ♀♀ from months of May and July.

QUEENSLAND: Low Isles, Murray I., Palm I., Port Denison, Hope I., Fairfax I., North West I., Heron I. NEW SOUTH WALES: Locality suspect.

Recorded habitats.—Intertidal, near or on coral structures, in shingle, and under living coral.

Material illustrated.—Carapace, basal antennal joint, male abdomen, male pleopod: ♂ 40 mm, Low Isles, 30.viii.54, W. Stephenson (Zool. Dept., Univ. Qld.).

Description

Front.—Six rounded lobes, medians slightly broader than the subequal laterals and frontals (ratio of breadths in profile view 8:7:7). Inner orbital lobes short and with obliquely sloping inner borders; between them and the lateral frontal lobes, spines on basal antennal joint are conspicuous in dorsal view.

Anterolateral teeth.—Five sharp teeth, 1st stoutest, 2nd and 3rd longest, 4th and 5th small and subequal.

Carapace.—Bearing usual 3 ridges on gastric region; of these, frontal and protogastrics relatively coarser and granular; mesogastric not interrupted in the mid line, and in 1 specimen (Qld. Mus. regd. No. W991), extended with a slightly anterior orientation on the left; epibranchial broadly interrupted at cervical grooves and also medially. Mesobranchial and median cardiac ridges absent. General surface of carapace highly polished, and microscopically pitted. In front of epibranchial ridge, scattered feathered hairs, particularly concentrated between bases of anterolateral teeth and in region between protogastric ridge and orbit.

Basal antennal joint.—Relatively long, *c.* 1·65 times major diameter of orbit, bearing 2 or 3 spines in centre of crest, followed by short irregular clump of 4 or 5 granules.

Chelipeds.—Right cheliped larger, spines long and sharp, upper surfaces with conspicuous rounded tubercles. Anterior border of arm bearing 3 long curved spines; the 3 spines on outer wrist margin sharper and more definite than usual, as are the 4 spines on upper surface of hand. On outer surface of the hand, middle and lower carinae are sharp and very distinct with the middle one composed of closely fused tubercles. Uppermost carina represented by incomplete row of large, rounded tubercles. From middle carina to inner edge of upper surface of hand there are large, scattered, rounded tubercles, amongst which lie feathered hairs. Inner surface of hand with very indistinct and rounded prominence, corresponding with a median carina; apart from this, inner and lower surfaces smooth and highly polished. Fingers long, sharp, and deeply grooved.

Fifth leg.—Merus stout, twice as long as broad, with usual spine at posterior border; posterior border of propodus bearing 4 large and 3 small spines.

First male pleopod.—Elongate, slightly curved, swollen near middle and tapering quite strongly to tip. Inner surface bearing 3 or 4 fine hairs just before the swollen portion, and from there onwards are sparsely arranged, minute, inconspicuous spinules merging into the terminal, or more strictly the subterminal, bristling which consists of 2 indistinct rows of moderate-sized bristles. Outer armature begins as sparsely arranged bristles which become longer and more crowded towards tip where *c.* 15 are visible in profile view. There are in addition 3 large, blunt, rounded, tubercle-like spines immediately behind tip.

Colour alive (based on 1 specimen).—Orange edges to frontal lobes, blue-green chelipeds with brown spots. After alcohol preservation, dorsal surface dull orange with mottlings of brighter orange and brick red. These red markings regularly arranged, particularly on epibranchial ridge and immediately in front of mesogastric ridge. Upper surface of hand bearing orange-red spots, conspicuous on the outer surface, particularly on median carina. Anterolateral teeth and spines of chelipeds orange-coloured at bases, pale near tips, and then sooty brown at tips. Walking and swimming legs uniform biscuit colour.

Comments

The similarity between this species and *Thalamita spinimana* has long been recognized. Thus A. Milne Edwards (1861, pp. 363–4) could separate them only by the increased number of spines on the arms of *T. spinimana* as against *T. coeruleipes*. In *T. coeruleipes* there are the 4 usual spines on the upper surface of the hand (excluding the spine at the wrist articulation), whereas there are 5 spines, 2 on the outer row but *three* on the inner row, in *T. spinimana*.

In addition, the carapace of *T. coeruleipes* is relatively longer than that of *T. spinimana*. In *T. coeruleipes*, the ratio of breadth/length is 1·48 (♂, Mijake 1939, p. 171), 1·47 (♀, Mijake 1939, p. 171), 1·48 (illustrated specimen of present work); whereas in *T. spinimana* the ratio is 1·6 (calculated from A. Milne Edwards (1861, Plate 4, Fig. 5) and from Shen (1937, Fig. 17*a*).

On this basis, Milne Edwards's (1861) description of *T. coeruleipes* is barely accurate enough in that the length/breadth ratio is given as approximately two-thirds. In addition, he states that the 3rd anterolateral tooth is "un peu plus petite que les autres" which is possibly a typographical error. Mijake (1939, p. 171) states that the anterolateral teeth are "successively decreasing in length" but from his figure, the 4th and 5th would appear to be distinctly smaller than the remainder and subequal. The 2 species can be further separated by the form of the male abdomen (see Mijake 1939, Fig. 1*c*; Shen 1937, Fig. 17*b*), and by the male pleopods.

Distribution

Previously known from the Indian Ocean, viz. Mauritius (Ward 1942), and tropical and subtropical West Pacific, viz. Celebes (de Man 1895); Mangavera I., Pacific Ocean (A. Milne Edwards 1861); Gilbert Is. (Holthuis 1953); Oahu (Rathbun 1906), Fiji Is. (Balss 1938); now Australia.

Specimen resembling T. coeruleipes

Plate 2, Fig. 2; Plate 7*E*

A small fragmented ♂ (10 mm, Bowen, Pt. Denison, pres. May 1921, E. H. Rainford, Aust. Mus. regd. No. P5206) is referred to *T. coeruleipes* but with some uncertainty. The main differences are broader submedian frontal lobes, broader orbits, longer carapace, less distinct carapace ridges, 4th anterolateral tooth smaller than 5th, basal antennal joint shorter than width of orbit (0·87), less conspicuous granulation of chelipeds, and relatively shorter ultimate and penultimate segments of the abdomen.

All these features, with the possible exception of the size of the 4th anterolateral tooth, could well be due to juvenility. It is significant that small specimens referred to other species (*T. crenata* and *T. stimpsoni*) again have small 4th teeth.

The specimen is not included in the key, but comes down under 15(14) as *T. danae*, from which it is easily separated by the inclination of the inner orbital lobes.

Thalamita cooperi Borradaile

Plate 1, Fig. 4; Plate 10*C*

Thalamita cooperi Borradaile, 1902, pp. 206–7, fig. 37.

Material Examined

QUEENSLAND: At Aust. Mus.: ♀ 9 mm, Aug.–Oct. 1907, C. Hedley and A. R. McCulloch (regd. No. P7546); ♀ 11 mm,* (under stones, near shore, reef), Lady Musgrave I., Bunker Grp., 1926, M. Ward; ♀ 10 mm,† Murray I., Torres Str., Oct. 1928, M. Ward (regd. No. P12754).

Material illustrated.—Starred specimen above. Male abdomen and pleopods were not available.

Description (based on specimen†)

Front.—Four-lobed, medians much broader than laterals (*c.* 5 times), slightly sinuous. Inner orbital lobes short and arched.

Anterolateral teeth.—Four, sharp, subequal, last the smallest.

Carapace.—Three usual pairs of gastric ridges, also epibranchial which is uninterrupted at cervical grooves. A sinuous cardiac present, and on either side 3 closely spaced inconspicuous parallel mesobranchials. Apart from these, carapace sparsely covered with long fine hairs.

Basal antennal joint.—Shorter than orbit (*c.* 0·86 times), bearing short, sharply elevated ridge, tipped by fused granules.

Chelipeds.—Subequal granular, with long fine hairs between granular regions. Anterior border of arm, wrist, and upper surface of hand with usual spines, all acute and well developed. The 2 lowermost carinae on outer surface of hand present and conspicuously granulated, and a low granular ridge corresponds to carina on inner surface of hand. Lower surface of hand bears squamiform markings.

Fifth leg.—Merus unusually long (thrice as long as broad), bearing usual spine. Five or 6 long spines on posterior border of propodus.

First male pleopod.—Unknown.

Comments

The specimen from Murray I. differs from that figured in having the front more rounded and the anterolateral teeth stouter and blunter.

The described specimen agrees precisely with Borradaile's description, in which the main omissions concern the ridges of the posterior part of the carapace. In the remaining specimens, a vestigial 4th anterolateral tooth is present, and this is one of the two characters which separated *T. cooperi* from *T. invicta* Thallwitz. The only character now separating them is the presence of 5 spines on the hand (including that at the wrist articulation) in *T. cooperi* as against 3 in *T. invicta*. Until the type of *T. invicta* can be re-examined, it seems convenient to maintain their separation.

Distribution

Maldive and Laccadive Archipelago (Borradaile 1902); now Queensland.

THALAMITA CRENATA (Latreille)

Figs. 2*Q*, 3*Q*; Plate 2, Fig. 3; Plates 7*F*, 9*C*

Portunus crenatus Latreille, 1829, fide Milne Edwards, H., 1834.

Thalamita crenata Milne Edwards, H., 1834, p. 461. Milne Edwards, A., 1861, pp. 365, 367. Alcock, 1899, pp. 76–7 (lit. and synon.). Nobili, 1906*a*, pp. 201, 202. Stimpson, 1907, pp. 84–5, pl. X, figs. 6, 6*a*. Stebbing, 1910, pp. 309–10. Rathbun, 1910*a*, p. 365. Kemp, 1915, p. 249. Sakai, 1936, p. 161, pl. 12, fig. 2; 1939, pp. 413–15, pl. LXXXIV, fig. 3. Shen, 1937, p. 129, fig. 16*a*, *c*, *d* (male abdomen in 16*b* is unduly broad). Barnard, 1950, pp. 172, 174, figs. 27*e*, 33*a*. Edmondson, 1954, pp. 267–9, figs. 39*b*, 40*a–f*.

Thalamita prymna var. *crenata* Laurie, 1906, p. 418.

Material Examined

46 ♂♂ (13–75 mm); 35 ♀♀ (25–71 mm). Smallest ovigerous ♀ 37 mm; ovigerous ♀♀ from Aug. to Jan., noted as especially common in Oct. 1953 in Moreton Bay.

QUEENSLAND: Moa I., Murray I., Badu I., Goode I., Flinders I., Endeavour R., Woody I., Low Isles, Kent I., Palm I., Cardwell, Townsville, Magnetic I., Port Denison, Whitsunday Passage, Lindeman I., Hamilton I., Cannonvale, Facing I., Gladstone, Port Curtis, Bundaberg, Pialba, Moreton Bay (Scarborough, Green I., Dunwich, Southport). WESTERN AUSTRALIA: Exmouth Gulf. NORTHERN TERRITORY: Groote Eylandt, Sir Edward Pellew Grp., Indian I., Darwin.

Recorded habitats.—Intertidal, mud flats, under stones, boulders, and mussel clumps, also mud banks, near mangroves, very occasionally amongst coral near the mainland.

Material illustrated.—Carapace, basal antennal joint, male abdomen: ♂ 58 mm, Dunwich, Moreton Bay, 30.v.52, coll. Miss J. Teys. Male pleopod: ♂ 63 mm, Airlie Bay, near Cannonvale, 21.viii.52, coll. Zool. Dept. party; ♂ 24 mm, Port Langdon, Groote Eylandt, 11.xi.53, coll. D. J. Tranter. (All Zool. Dept., Univ. Qld.).

Description

Front.—Typically 6 lobes, rarely reduced by fusion of median and submedian lobes, which may be complete or only affect 1 side. In typical forms, lobes vary from round, protruding, tongue-shaped structures to relatively broad low lobes. Medians slightly the broadest, lying only on a very slightly lower plane than remainder; laterals

usually the smallest. Inner orbital lobes distinctly arched and approximately as broad as combined widths of submedian and lateral frontal lobes.

Anterolateral teeth.—Five, subequal, decreasing slightly in size from front to rear.

Carapace.—Gastric and epibranchial ridges normal, carapace otherwise perfectly smooth, except in recently moulted specimens. Here there are fine hairs, sparsely arranged near anterolateral teeth and protogastric ridge. Posterolateral angles slightly more obtuse than right-angled.

Basal antennal joint.—Much wider than orbit, from 1·7 times (specimen 44 mm broad) to 1·98 times (specimen 73 mm broad); bearing a low ridge, with sparse, rounded granules or tubercles which are larger and tend to be fused immediately below flagellum insertion.

Chelipeds.—Right more massive than left, having smoother rounded surfaces. Anterior border of arm sometimes with 4 spines. Wrist with spines normal and upper surface bearing patch of scattered granules on anterior third. Normal 3 spines present on upper surface of hand, and position of 4th (anterior outer) indicated by blunt tubercle. Outer margin of upper surface of hand bearing granules, arranged in irregular vertical rows. Outer surface of hand smooth and shining, bearing single crest running to tip of movable finger. Inner surface of left cheliped only, with broad anterior eminence, presumably rudiment of a carina. Under surface strongly granular on inner side just in front of wrist articulation, the granulation fading away distally. Fingers less conspicuously grooved than normal, with no groove on under surface of immovable finger, 1 groove on outer side of each finger, and 1 on inner side of each finger; also short groove on upper surface of movable finger.

Fifth leg.—Merus *c.* 2·2 times as long as broad, smooth except for usual spine on posterior border. Posterior margin of propodus bearing *c.* 5 distinct spines, remaining 4–6 being small inconspicuous tubercles.

First male pleopod.—Long, thin, gradually tapering, smoothly curved with obliquely opening tip. Inner surface with inconspicuous, short, forwardly directed spinules from about one-quarter of the way up from base. These merge into an indistinct double row of bristles near tip. Outer side without ornamentation up to tip. *Terminal bristles.*—On inner surface, none; on outer side, 5 pairs (last 3 very close together), followed by a confused clump of *c.* 6 bristles, followed by 2 small spines.

Colour.—After prolonged alcohol preservation, faded brown on tips of anterolateral teeth and spines of chelipeds. Alive, predominantly brownish green.

Comments

The frontal teeth of this species show a surprising plasticity, necessitating duplicate appearances of the species in the key. Its most characteristic feature is the massive, smooth, rounded chelipeds. Sakai's diagnosis (1939, p. 414) contains a typographical error in giving 6 anterolateral teeth.

A small ♂ (14·5 mm, mud flats, M.L.W., Dunwich, Moreton Bay, 27.vi.53, W. Stephenson) not included in the above records is doubtfully referred to the present species. This specimen is atypical in: (*a*) having on the right 4 anterolateral teeth, and on the left 5 teeth with the 4th noticeably smaller than the 5th, and (*b*) the basal antennal joint being only 1·06 times the major diameter of the orbit, as compared

with a range of 1·7–1·98 times in specimens 44–73 mm. Although a low value could be expected for a small specimen, the present ratio seems extremely small.

Distribution

Published and present records within Australia are from Queensland (Miers 1884, 1886; Ortmann 1894; Whitley and Boardman 1929; Stephenson *et al.* 1931); New South Wales (Ward 1937); Western Australia (Rathbun 1924); now Northern Territory.

Outside Australia, from Durban to the Red Sea in the west, and from Japan to the Society Is. in the east (Miers 1884; Alcock 1899; Rathbun 1921; Sakai 1939; Barnard 1950).

Thalamita dakini Montgomery

Plate 2, Fig. 4; Plate 9*D*

Thalamita dakini Montgomery, 1931, pp. 432–3, pl. 24, fig. 3, pl. 28, fig. 4.
? *Thalamita medipacifica* Edmondson, 1954, pp. 260–2, figs. 34*a*, *b*, 35*a*.

This is the only Australian species not examined by the authors and is known only from the holotype in the British Museum. The original description is cited below, and copies of original illustrations are given.

"*Locality.*— 1 ♂, Wooded Island, Abrolhos.

"Measurements (in mm.):

C.l.	11
C.b.	18
Posterior border of C.b.	6
Basal antennal joint b.	3·5
Major diam. of orbit	2·5
Middle frontal lobe b.	2·5

"This species further complicates the problem of the genus *Thalamita*. The striking features are the basal antennal joint and the front. As is shown above, the extreme extent of the basal antennal joint is neither 'far greater than the major diameter of the orbit' nor is it 'equal to or less' (Alcock, 1899*a*, p. 73). The proportion between the breadth of the basal antennal joint and the carapace breadth is 2:9 in *T. prymna* var. *crenata*, 1:4 in *T. prymna* and *T. admete*, 1:5 or 6 in *T. chaptalii*; and in *T. investigatoris* it is less than, in *T. imparimanus* less than half, and in *T. sexlobata* about equal to the major diameter of the orbit. *T. dakini* agrees, therefore, in this respect most nearly with *T. chaptalii*.

"There is a ridge of granules on the basal antennal joint. The orbits have a slight dorsal inclination as in *T. sexlobata* (Miers, 1886) and *T. oculea* (Alcock, 1899*a*).

"The front is four-lobed, excluding the inner orbital lobe, but the two lateral lobes are very small and are minutely toothed at their margins; from these a line of granules continues on in the line of the front beneath the inner supraorbital lobe, between it and the extension into the orbit of the basal antennal joint. The front is thus unique among the Thalamitas.

"The inner supraorbital lobes are slightly concave forwards, and each is about equal in extent to the middle frontal lobes, though disposed on an alignment behind

and above these; the front is slightly flexed downward. The carapace is hairy and the lines of the carapace are disposed much as in *T. admete*. The teeth of the antero-lateral border are five in number, the fourth being small. The posterior border of the carapace is straight and about one-third the greatest breadth of the carapace.

"The chelipeds are smooth on the inner and lower borders, spined, granular, costate, and hairy on the upper and outer surface. The spines are disposed as in *T. sima* with the addition of an extra large spine on the upper border of the hand; the spines are everywhere sharper and the granules tend to be spiny.

"The hands bear three costae on the outer surface, which are granular, the granules tending to be sharp. The fingers are stumpy, but strongly denticulated.

"The legs are stout and costate; the propodite of the last pair of legs is hairy, but not spined.

"*Distribution.*—Abrolhos, W.A."

Comments

T. medipacifica appears to be identical with *T. dakini*, both sharing a very characteristic form of the front. Thus Montgomery's Plate 28, Figure 4, is almost identical with Edmondson's Figure 34*d*, and certainly within the range of figures Edmondson gives. The differences between the 2 forms appear to be:

(*a*) Basal antennal joint with a ridge of granules in *T. dakini* against a line of 4 or 5 small tubercles in *T. medipacifica*. This difference may well be in the words used rather than the structures themselves.

(*b*) Inner orbital lobes with a slightly concave front margin in *T. dakini* as against a slightly convex margin figured for *T. medipacifica* (Edmondson). However, Edmondson's photograph (Fig. 35*a*) suggests slight concavity.

As the authors have not examined specimens of this species, inclusion of *T. medipacifica* in the synonymy remains tentative. If it is so included the description of *T. dakini* needs amplification, especially to cover variations in the lateral portions of the front.

THALAMITA DANAE Stimpson

Figs. 2*N*, 3*N*; Plate 3, Fig. 1; Plates 7*G*, 10*D*

Thalamita crenata Dana, 1852*a*, p. 282, pl. XVII, fig. 7*a*, *b* (non Latreille 1829).
Thalamita danae Stimpson, 1858, p. 39 (nom. nov.). Milne Edwards, A., 1861, pp. 366–7, pl. XXXVI, fig. 1. Miers, 1876, p. 29. Alcock, 1899, pp. 77–8 (lit. and synon.). Stimpson, 1907, p. 85, pl. XI, figs. 1, 1*a*. Shen, 1934, pp. 52–4, figs. 15, 16 (excluding synon.). Sakai, 1939, pp. 413, 415, pl. LXXXV, fig. 3. Barnard, 1950, p. 174.
? *Thalamita danae* de Man, 1887, p. 78, pl. IV, figs. 8, 9.

Material Examined

10 ♂♂ (25–73 mm); 4 ♀♀ (20–66 mm).

NORTHERN TERRITORY: Darwin, Port Essington, Sir Edward Pellew Grp., Groote Eylandt.

Recorded habitats.—Sandy mud flat, amongst rocks on shore.

Material illustrated.—Carapace, basal antennal joint, male abdomen: ♂ 58 mm, Observation I., Sir Edward Pellew Grp. (Aust. Mus. regd. No. P6576). Male pleopod:

(1) as above; (2) ♂ 36 mm, Port Langdon, Groote Eylandt, 11.xi.53, D. J. Tranter (Zool. Dept., Univ. Qld.).

Description

Front.—Six-lobed, median pair with truncate anterior margins and *c.* 1½ times breadth of submedians and laterals as seen in profile view; submedians directed anterolaterally and separated from laterals by deep groove. Inner orbital lobes broad, and approximately width of frontal lobes.

Anterolateral teeth.—Five, all stout, 1st largest, 2nd and 3rd subequal, 4th and 5th slightly smaller, 4th slightly smaller than 5th.

Carapace.—Apart from ridges, dorsal surface almost completely covered with short thick fur. Usual ridges present; epibranchial interrupted at cervical groove but not medianly; mesobranchial and cardiacs merely smooth areas amongst the hair. Cardiac has curved anterior extensions which almost join epibranchials.

Basal antennal joint.—Very much wider than major diameter of orbit, almost exactly twice (in ♂ 58 mm); bearing sharp ridge which carries beaded granules with distal row of *c.* 11 which are reasonably spaced, and continuing as proximal row of 4 to 6 closely spaced granules.

Chelipeds.—Right slightly the larger. Anterior border of arm and wrist with usual spines. Latter short and stout, corresponding carinae well marked, upper surface of the wrist densely covered with fine hairs. Four usual spines on upper surface of hand; the 2 innermost being terminations of very distinct carinae with finely granular edges. Carinae on outer surface conspicuous, the 2 lowermost with granular edges. Upper carina granular distally and smooth and rounded proximally. Between carinae the usual hairy pile beneath which are rounded granules, more conspicuous towards upper surface. Inner surface of hands bearing rounded median carina above which is an irregular granular row, remainder covered with hairs. Boundary between inner and lower surfaces distinct but barely distinct enough to form keel, lower surface traversed by fine irregular furrows.

Fifth leg.—Merus short and broad (length *c.* 1·9 times breadth), 10–12 smallish spines on posterior border of propodus.

First male pleopod.—Smoothly curved, regularly tapering with blunt oblique tip. On inner surface, minute spinules begin about half way up, become progressively longer, and merge with subterminal armature, which consists of pairs of moderately sized hairs. Subterminally, a series of regularly and somewhat distantly spaced fine bristles, becoming stouter towards tip, here merging into a clump, showing 11 bristles in profile view. Two stout, conical spines visible near end of clump.

Comments

To judge from past descriptions there are variations in the detailed structure of the frontal lobes and also in the male abdomen. Thus Milne Edwards's (1861) and de Man's (1887) figures of the frontal lobes show them more uniformly rounded than in Shen's (1934) figures or in the present specimens. The figures of Milne Edwards (1861) and de Man (1887) and the descriptions of Alcock (1899) and Barnard (1950) indicate that the penultimate segment of the male abdomen is much broader

than long, while in the present specimen and in Shen's (1934) figure it is only slightly longer.

According to Miers (1880, p. 238) there are also variations in the length of the 4th anterolateral tooth. Confirmation of this variation is highly desirable, since the presence of a noticeable small 4th tooth is the only macroscopic character separating *T. danae* from *T. stimpsoni*. On the basis of the specimens examined, the separation into 2 species appears to be sound and is confirmed by the study of male pleopods. The separation has been acceptable to Sakai (1939), the most conspicuous recent worker on the genus in the Western Pacific.

Montgomery (1931, p. 430, in key) separates *T. danae* from *T. stimpsoni* by the presence of a faint granular ridge separating inner from lower surfaces of the hand. In the present specimens this ridge is barely detectable.

Distribution

In the west, from Mozambique to the Red Sea; in the east, from south Japan, the Marshall Is., Gilbert Is., and Fiji (Stimpson 1858; Milne Edwards 1861; de Man 1895; Alcock 1899; Dana, fide Doflein 1904; Laurie 1915; Shen 1934; Balss 1938; Sakai 1939; Barnard 1950; Holthuis 1953). There is a surprising record from New Zealand (Miers 1876; Heller, fide Doflein 1904) but the species had not been recorded previously from Australia.

Ecological notes given by Shen (1934) and Sakai (1939) indicate that the species lives under or amongst stones, as does the closely related *T. stimpsoni*.

THALAMITA INHACAE Barnard

Figs. 2*L*, 3*L*; Plate 3, Fig. 2; Plates 7*H*, 10*E*

Thalamita inhacae Barnard, 1950, p. 179, fig. 33*g*.

Material Examined

QUEENSLAND: At Zool. Dept., Univ. Qld.: 4 ♀♀ 13–21 mm, ♂ 15 mm,* E.L.W.S., amongst mussel clumps, Dunwich, 18.vi.55, T. Kirkpatrick and W. Hasseler; ♂ 17 mm, Pat's Pt., Moreton Bay, Nov. 1955, N. Haysom. At Aust. Mus.: ♂ 16 mm, Hope I., pres. A. R. McCulloch, Aug. 1913 (regd. No. P3801, here referred to as specimen A). At Aust. Mus., Great Barrier Reef Exped. Collections: ♂ 10 mm, at 19 fm, stn. xiv, ½ mile SE. Lizard I. (here referred to as specimen B, carapace only); ♀ 8 mm (specimen C), ♀ 8 mm (specimen D), at 20 fm, stn. xvi, dredged about ½ mile W. of N. Direction I.; ♀ 14 mm (specimen E), ♀ 13 mm (specimen F), ♂ 10 mm (specimen G), ♂ 10 mm (specimen H),* at 19 fm, stn. xvii, trawled, about ¼ mile N. of N. Direction I. NEW SOUTH WALES: At Aust. Mus.: ♀ 13 mm, among growth on hull of H.M.A.S. *Penguin*, when in dock, Cockatoo I., Port Jackson, pres. April 1926, G. P. Whitley and A. A. Livingstone (regd. No. P8564); ♀ 8 mm, Shellharbour, pres. 1923, G. McAndrew (originally with regd. No. P6301). LORD HOWE I.: At Aust. Mus.: ♂ 15 mm, ♀ 10 mm, ♀ ovigerous 9 mm, at 4 fm, pres. April 1933, A. A. Livingstone.

Material illustrated.—Carapace, male pleopod, male abdomen: ♂ 10 mm (specimen H starred above). Basal antennal joint: ♂ 15 mm, Dunwich, starred above.

Description

Front.—Four-lobed; quadrate inner lobes separated by a small cleft and approximately twice (1·8–2·3) length of outer; inner orbital lobes very slightly arched, arching being more obvious in smaller specimens, and about four-fifths of breadth of median frontal lobes.

Anterolateral teeth.—Four; 3rd rudimentary and mainly represented by the considerable interval between 2nd and 4th; 1st stoutest but more slender than in Barnard's figure; 2nd small and sharp, 4th sharp and projecting slightly more than the others.

Carapace.—Reasonably elongated, smooth and round, breadth 1·35–1·5 times length. Only epibranchial ridges present, these only extending inwards one-quarter of carapace width, leaving central half smooth; marked depression between the 2 indistinct cervical grooves. Inner orbital lobes elevated above general surface, arising from unusually distinct curved grooves which sometimes bear inconspicuous soft hairs. Posterolateral extremity obtusely rounded.

Basal antennal joint.—Less than major diameter of orbit (0·66–0·92), bearing short smooth curved crest.

Chelipeds.—Right normally distinctly larger than left (the reverse in specimen F). Anterior border of arm with proximal spine sometimes reduced to a tubercle. Usual spine present on antero-external angle of wrist, and 3 indistinct tubercles representing spines on outer surface. Surface of wrist minutely granular in freshly moulted specimens, but normally perfectly smooth and bearing traces of a carina corresponding to outer tubercles. Hand bearing usual spine at wrist articulation, spine on middle of inner side of upper surface, and 3 blunt spines or tubercles—at distal end of inner side of upper surface, and also near and at distal end of outer side, respectively. These spines, especially the sharp one on the inner surface, mark terminations of carinae. No carinae on any other surfaces of hand except the usual one on lower part of outer surface, which continues to tip of immovable finger.

Fifth leg.—Merus 2·6–3·2 times as long as broad, smooth posteriorly apart from a single spine. Posterior border of propodus bearing 4–10 sharp spines.

First male pleopod.—Short, very stout, only slightly curved, tip ending obliquely and abruptly. Beyond the basal lobes bare until terminal bristles. *Terminal bristles on inner side.*—Short stout conical spines, 6–7 visible in profile view, numerous additional ones apparent in a cleared stained preparation. Behind these, a few irregularly arranged spinules. *Terminal bristles on outer side.*—Twelve to 14, arranged somewhat irregularly, but with longest and stoutest bristles just behind tip. All inclined distally and parallel to oblique tip of appendage.

Colour.—After 25 years in alcohol, pale biscuit colour, fading to ivory on chelipeds and legs.

Comments

These specimens differ from Barnard's description in the following minor particulars:

(*a*) Inner orbital lobes are slightly arched in the present specimens but described as straight in *T. inhacae*.

(*b*) First anterolateral tooth is sharper in the present specimens.

(*c*) The epibranchial ridges in the present specimens are shorter than those figured for *T. inhacae*.

(*d*) The merus of the 5th leg is roughly thrice as long as broad in the present specimens, as compared with slightly more than twice in *T. inhacae*.

It is unfortunate that the original description of *T. inhacae* is based upon a single ♀, and therefore a critical comparison of male pleopods is impossible. Until such a comparison can be made on topotypical material a slight doubt must exist as to whether the present species is *T. inhacae* or an undescribed form.

Distribution

Known from Inhaca I., Delagoa Bay, south-east Africa (Barnard 1950); now from eastern Australia.

Thalamita integra Dana

Figs. 2*H*, 3*H*; Plate 3, Fig. 3; Plates 7*I*, 10*F*

Thalamita integra Dana, 1852*b*, p. 85. Stimpson, 1858, p. 39. Milne Edwards, A., 1861, pp. 358, 367. Miers, 1884, pp. 518, 540. De Man, 1887, pp. 74–5; 1902, p. 646. Henderson, 1893, p. 373. Alcock, 1899, p. 85 (lit. and synon.). Parisi, 1916, p. 177 (lit. and synon.). Rathbun, 1921, pp. 402–5. Sakai, 1939, pp. 414, 420–1, fig. 15, pl. LXXXIV, fig. 2 (lit.). Edmondson, 1954, pp. 252, 253–4, figs. 27*a–e*, 28*a*.

Material Examined

7 ♂♂ (11–39 mm); 7 ♀♀ (18–26 mm). Smallest ovigerous ♀ 18 mm; ovigerous ♀♀ from month of May.

QUEENSLAND: Heron I., North West I., Lady Musgrave I.

Recorded habitats.—Under small pieces of dead coral on sand; dredged 4–5 fm, coral sand.

Material illustrated.—Carapace, basal antennal joint, male abdomen, male pleopod: ♂ 28 mm, Heron I., Sept. 1926, coll. M. Ward (Aust. Mus. regd. No. P12762).

Description (based largely on 2 ♂♂ and 1 ♀)

Front.—Bilobed, in ♂♂ frontals sinuous, each with a lateral flange; in ♀♀ lobes almost smoothly curved. Inner orbital lobes straight, six-sevenths width of frontal lobes.

Anterolateral teeth.—Five, 1st largest, closely followed by 2nd and 3rd, all stout, generally blunt; 4th much the smallest and sharp, 5th sharp and protruding beyond the others.

Carapace.—Breadth 1·75 times length. Frontal ridges present as rounded elevations; protogastrics either unrecognizable or very faintly recognizable; mesogastrics distinct, almost straight; epibranchial well developed, interrupted at cervical grooves and medianly; median mesobranchial short but distinct; cardiacs not present.

Basal antennal joint.—Distinctly longer than orbit (1·3–1·5 times on specimens 20–28 mm); bearing short, elevated crest either smooth or minutely granular.

Chelipeds.—Right larger, both having smooth rounded surfaces; anterior border of arm bearing either 3 or 2 distinct spines preceded by rounded granules; wrist bearing

usual spine on inner margin but shorter and stouter than usual; spines on outer surface reduced to rounded tubercles, with distinct carina leading to lowermost. Surfaces of hand smooth and rounded, except for 2 carinae leading to immovable finger and on upper inner surface respectively. The latter very distinct and bearing 2 spines, the distal reduced to a rounded tubercle. Spine at wrist articulation much shorter than usual, often reduced to rounded tubercle. In the position of the obsolescent carinae on outside of upper surface of hand are 2 tubercles of which distal is barely recognizable. Fingers of right cheliped short and stout; those of left sharp and elongate.

Fifth leg.—Merus *c.* 1·75 times as long as broad; posterior margin of propodus bearing 6–9 spines, variations being in presence of small proximal spines.

First male pleopod.—Short, stout, practically straight, gradually tapering, with large, conspicuous backwardly directed bristles near tip which is barely enlarged. Beyond basal lobes bare in proximal half; and in distal half bearing minute anteriorly directed hairs or spinules. *Terminal bristles on inner side.*—Five or 6, increasing in length proximally and sharply inclined backwards, followed by the last, much the longest, projecting directly outwards. *Terminal bristles on outer side.*—Twelve, all except the most proximal strongly inclined backwards, and the 5th from the front (of those clearly visible), the longest. Behind the last bristle a stout forwardly directed hair, with a similar hair sometimes present on inner side, slightly further forwards.

Comments

The species differs minutely from the descriptions of Sakai (1939) and Edmondson (1954) in the possession, in larger specimens at least, of 2 short but distinct ridges on the mesogastric region of the carapace.

Rathbun (1921, pp. 402–4, Fig. 5 and Plate XXIII) separates as a distinct species *Thalamita africana*, which Miers (1881, p. 218) had originally described as being only a variety.

Rathbun quotes the following characters as evidence for specific status:

(*a*) Inner orbital lobes arcuate instead of straight. This is an inconspicuous character, and the most distinct plate given by Rathbun (Plate XXIII, Fig. 2) shows these lobes no more curved than in either Sakai's plate of *T. integra* or in the present specimens. Moreover, the left inner orbital lobe of Rathbun's Figure 5*c* is more straight than it is arcuate.

(*b*) Fourth anterolateral tooth small but not minute. This applies equally to the present specimens and evidently this feature is variable (see Edmondson 1954).

(*c*) Progastric regions each bearing a short granulated ridge. In the present specimens there are rounded elevations in this region, but no distinct ridge.

(*d*) Two spines on the upper edge of the hand blunt, not sharp. Sakai (1939, p. 421) describes these as "obliterated spines" and Edmondson (1954, p. 254) as "not well developed". In the present specimens their sharpness is variable, as it is in practically every species of the genus, depending no doubt upon the amount of wear.

It is concluded that only the third feature of the four quoted by Rathbun appears to have both constancy and significance, and that the elevation of the West African specimens to the status of a full species is undesirable.

Distribution

Sandwich Is., Tahiti, Paumatou (Milne Edwards 1861); Suez, Aden (fide Nobili 1906*a*); Amboina, Timor (de Man 1887); east Africa, Malay Archipelago, Fiji (Henderson 1893); Bonin I., Palao I., Hawaii, Polynesia, Malaya, India, Red Sea (Sakai 1939); Gulf of Manaar (Laurie 1906); Gilbert Is. (Balss 1938); now Queensland.

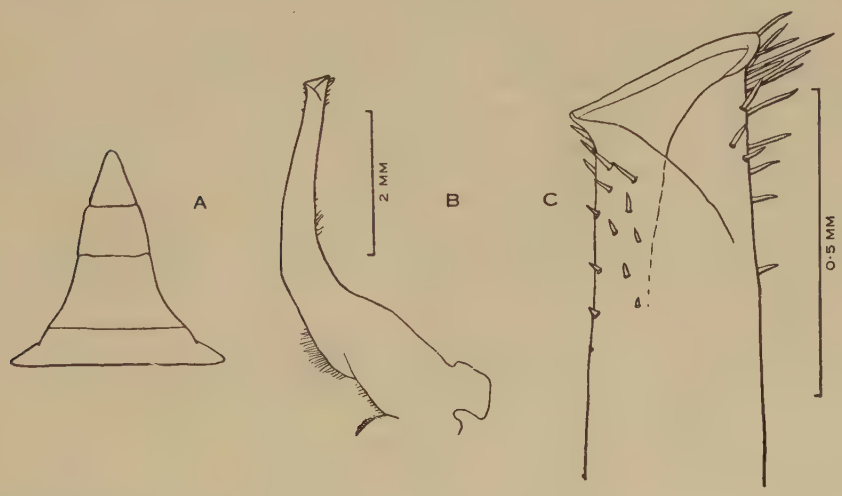

Fig. 4.—*T. intermedia*. *A*, male abdomen; *B*, male pleopod; *C*, tip of male pleopod.

Thalamita intermedia Miers

Fig. 4; Plate 3, Fig. 4; Plate 10*G*

Thalamita intermedia Miers, 1886, p. 196, pl. XVI, fig. 1. Ortmann, 1894, p. 46. Alcock, 1899, pp. 89–90. Rathbun, 1924, pp. 24–5. Hale, 1927, p. 151, fig. 152.

non *Thalamita admete* var. *intermedia* Borradaile, 1902, pp. 202–3. Nobili, 1906*a*, pp. 202, 208–9.

Material Examined

3 ♂♂ (11–21 mm); 6 ♀♀ (18–38 mm).

QUEENSLAND: Possession I., Endeavour Channel; Thursday I. WESTERN AUSTRALIA: Gantheaume Pt., Roebuck Bay, Broome, Ninety Mile Beach.

Recorded habitats.—On bamboo raft; in wire cage containing pearl-shell, 10 ft depth; dredged 4–8 fm; lithothamnion reef bottom.

Material illustrated.—Carapace, basal antennal joint: ♀ 18 mm, Possession I., Endeavour Channel, 11.ix.53, D. J. Tranter (Zool. Dept., Univ. Qld.). Male abdomen, pleopod: ♂ 21 mm, dredged 8 fm, Ninety Mile Beach, Broome, 1930, coll. Capt. R. Browne (Aust. Mus. regd. No. P9925).

Description

Front.—Four lobes demarcated by shallow indentations; medians projecting slightly more forward than laterals, and in profile view just over half breadth of laterals, outer border of laterals pointing directly forward. Inner orbital lobe scarcely arched and about 0·9 breadth of lateral frontal lobes in profile view.

Anterolateral teeth.—Five, 1st stoutest, 2nd and 3rd large and subequal, 4th and 5th small, 4th smallest.

Carapace.—Apart from indistinct ridges, completely covered with dense fine fur, removal of which reveals highly polished surface with microscopic pitting. At first sight, only mesogastric and epibranchial ridges present, but on removal of hairs traces of all normal ridges detectable. Frontals and protogastrics represented by granular eminences, while mesogastrics, broadly separated in mid line, are concave anteriorly. Epibranchials broadly interrupted in mid line, in region of cervical groove, and over branchial region proper; thus forming on each side, 3 distinct and broadly separated ridges. Cardiac ridge represented by 2 indistinct eminences; single mesobranchial ridge barely detectable.

Basal antennal joint.—Slightly wider than orbit (1·12 times). Crest bearing *c.* 20 rounded granules in an irregular, or bilinear, rather than linear arrangement.

Chelipeds.—Right slightly the larger, both conspicuously granulated and covered with fine hairs. Anterior border of arm and wrist with usual spines. Upper surface of hands bearing 4 usual spines on right, but anterior outer spine missing on left. These spines usually prominent, sharp, and separated by dense piles of hair. Outer surface of hand bears 3 carinae, lowest consisting of a single row of flattened granules, and middle and upper ones of several rows, irregularly arranged in the upper row. Inner surface of cheliped without distinct carina and covered by squamiform markings, which are continued to under surfaces and separated by line of hairs. Fingers long, sharp, and deeply furrowed.

Fifth leg.—Merus twice as long as broad with usual posterior spine; posterior border of propodus bearing 8–9 spines.

First male pleopod.—The 3 ♂♂ examined were received after the manuscript had been accepted for publication, and figures of pleopods and abdomen are given in a separate figure (Fig. 4). Short, stout, practically straight. Tip terminating obliquely with slight flaring. Outer surface with bristles in basal quarter and again in distal quarter, but sparse or missing between. *Terminal bristles.*—Continuous from inner to outer surfaces. Inner surface with *c.* 10 short bristles visible in profile view, arranged in indistinct rows pointing distally and increasing in length towards tip. Outer surface with *c.* 15 bristles visible in profile view becoming denser and longer towards the tip.

Colour.—After 2 months in alcohol, flesh-coloured, with tips of anterolateral teeth, and spines of chelipeds, pinkish orange. Centre of fingers sooty brown, tips ivory.

Comments

This species resembles *Thalamita malaccensis* Gordon (1938) and also *T. sexlobata* Miers (1886), in the following combination of characters:

(*a*) Four-lobed front, with median lobes narrower than laterals, and also more prominent;

(*b*) Basal antennal joint granular.

It differs from *T. sexlobata* in having narrower median frontal lobes and narrower longer carapace, and in having a moderately large, as against rudimentary, 4th anterolateral tooth. It differs from *T. malaccensis* in that the front of the latter is incipiently 6-lobed, or alternatively that the lateral frontals are concave anteriorly. In addition, the median frontal lobes are more prominent in *T. malaccensis*, where the basal antennal joint is "a trifle less" than the major diameter of the orbit.

Rathbun (1924, p. 25) states: "This little specimen, only 4·4 mm. long and 6·4 mm. wide, appears to be a young *intermedia*; it differs from the larger ones in having the inner supraorbital angles a little narrow proportionally and the basal antennal segment also narrower, in fact, narrower than the greatest diameter of the orbit".

Distribution

Mostly from Australian waters, viz. Torres Str. region (Miers 1886; Ortmann 1894; present records); South Australia (Hale 1927); Western Australia (Rathbun 1924; present records). A recent queried record by Holthuis (1953) is from the Marshall Is.

Thalamita macropus Montgomery

Figs. 2*J*, 3*J*; Plate 4, Fig. 1; Plates 7*J*, 10*H*

Thalamita macropus Montgomery, 1931, pp. 431–2, pl. 24, fig. 4, pl. 28, fig. 2 (inaccurate in 2*a*).

Material Examined

10 ♂♂ (4–27 mm); 7 ♀♀ (5–16 mm).

NEW SOUTH WALES: Port Stephens, Norah Hd., Pt. Gibbon, Manly.

Recorded habitats.—Dredged or trawled, 4 to *c.* 50 fm.

Material illustrated.—Carapace, male abdomen: ♂ 24 mm, Port Jackson, pres. Nov. 1908, old coll. (Aust Mus. regd. No. P1419). Basal antennal joint, male pleopod: ♂ 27 mm, Port Stephens, Jan. 1920 (Aust. Mus. regd. No. P4862).

Description

Front.—Six lobes widely separated; medians rounded; submedians flattened and almost twice as broad as medians; laterals rounded, triangular, slightly more than half breadth of medians; inner orbital lobes sharply curved.

Anterolateral teeth.—Five sharp teeth, borne on inclined borders, in general decreasing in size and increasing in sharpness from front to rear; but with 5th longer than 4th. Two-thirds of the way down 1st tooth, a secondary projection forming a minute subsidiary basal "tooth"; sometimes tooth-like, but more often merely an interruption in curvature of outer surface.

Carapace.—Closely beset with fine hairs through which ridges show conspicuously. Frontal ridges short, merely a cluster of granules; protogastrics an interrupted row of coarse granules; mesogastrics straight and broadly interrupted in the mid line;

epibranchials broadly interrupted at cervical groove, and narrowly interrupted in the mid line; 3 mesobranchial ridges, first 2 always distinct and last only occasionally so; 2 ridges, broadly separated, on cardiac region.

Basal antennal joint.—Much shorter than orbit (0·6–0·8 of its diameter in larger specimens), bearing a curved ridge with rounded granules.

Chelipeds.—In ♂ (only), right larger than left, and with stumpy fingers. Hand swollen, and upper surface of cheliped bearing rounded granules. Spines on arm, wrist, and hand normal. Carina on inner side of upper surface indistinct and represented by row of granules. Two similar rows on outer surface. Inner and under surfaces smooth, apart from carinae running to the immovable finger.

Fifth leg.—Merus twice as long as broad, with usual spine; posterior border of propodus with 5–10 spines.

First male pleopod.—Regularly curved and sickle-shaped. General bristling continuous with the terminal. *Terminal bristles on inner side.*—Two small spinules, set back from tip. *Terminal bristles on outer side.*—Two separate and parallel rows, *c.* 18 per row. Those at each end smallest; those on middle are short but stout, slightly inclined backwards. Tip scarcely swollen, with the opening an extremely oblique angle.

Comments

In the smaller specimens (Aust. Mus. regd. No. P11496) the 4th anterolateral tooth is extremely small and the distinction between the frontal lobes tends to disappear, particularly the separation between the submedians and laterals. The anterolateral margins and carapace ridges of this species are distinctive.

This species is discussed in Section III.

Distribution

Previously known only from East Wallaby I., Abrolhos (Montgomery 1931); now from New South Wales.

Thalamita picta Stimpson

Figs. 2*A*, 3*A*; Plate 4, Fig. 2; Plates 8*K*, 10*I*

Thalamita picta Stimpson, 1858, p. 39. Milne Edwards, A., 1861, pp. 362–3, 367; 1873, p. 164, pl. IV, fig. 4. Miers, 1884, pp. 518, 540. Alcock, 1899, p. 79 (lit. and synon.). Stimpson, 1907, pp. 85–6, pl. X, fig. 5. Shen, 1937, p. 135, fig. 19. Sakai, 1939, pp. 413, 417, pl. LI, fig. 2. Edmondson, 1954, pp. 253, 263–4, figs. 35*b*, 36*e–h*.

Thalamita prymna var. *picta* Borradaile, 1902, p. 201.

Thalamita gardineri Borradaile, 1902, pp. 205–6, fig. 36. Rathbun, 1911, p. 209.

Thalamita alcocki de Man, 1902, pp. 646–50. Edmondson, 1954, pp. 264–5, fig. 37*a*, *b*.

Charybdis picta Ward, 1934, pp. 9–10.

?*Thalamita investigatoris* Alcock, 1899, pp. 85–6. Alcock and Anderson, 1900, p. viii, pl. xlvii, figs. 1, 1*a*. Laurie, 1906, p. 420.

Material Examined

26 ♂♂ (10–30 mm); 15 ♀♀ (9–20 mm). Smallest ovigerous ♀ 18 mm; ovigerous ♀ from July.

QUEENSLAND: Murray I., High I., Capricorn Grp. (Heron I., Lady Musgrave I., One Tree I., North West I., Wilson I.), Caloundra, Moreton Bay. NEW SOUTH WALES: Angourie, Narrabeen, Port Jackson, Collaroy. LORD HOWE I.

Recorded habitats.—Under dead coral boulders, and under coral, fringing reef and near coral cays.

Material illustrated.—Carapace: ♂ 20 mm, pres. May 1908, Capt. T. Nichols (Aust. Mus. regd. No. P443). Basal antennal joint, male abdomen, male pleopod: ♂ 21 mm, NE. Heron I., 10.viii.50, W. Stephenson (Zool. Dept., Univ. Qld.).

Description

Front.—Six-lobed; medians the most projecting, rounded and distinctly separated from broader submedians whose outer edges point directly forward: laterals small and rounded, separated from submedians by deep indentation. Inner orbital lobes short and markedly arched.

Anterolateral teeth.—Five, 1st distinctly largest, 4th smallest; 2nd and 3rd stout; 5th sharpest and slightly protruding.

Carapace.—Longer than usual, breadth 1·4 times length. Three pairs of gastric ridges, well developed, also the epibranchial interrupted at cervical grooves. Cardiac and 2 mesobranchials well developed, posterior mesobranchials in line with cardiac. Apart from these ridges, carapace covered with fine hairy felting.

Basal antennal joint.—Ranging from very slightly wider to distinctly less than width of orbit (*c.* two-thirds), dependent on size of specimen; bearing an acute raised crest, typically smooth in larger specimens, with beaded granules in fairly small specimens, and with denticular granules in small specimens.

Chelipeds.—Right more massive than left. Anterior border of arm bearing 3 usual spines (very occasionally 4) as does wrist, whose innermost spine is unusually well developed. Upper surface of hand bears 4 usual spines, although outer distal one often reduced to tubercle. Granulation of wrist and hand, and also distinctness of carinae on hand, variable. In some specimens (equivalent to *Thalamita gardineri*) upper surface of hand bearing rounded granules, and inner surface squamiform markings, whereas in others, squamiform markings not detectable. Outer surface typically bearing the 3 usual carinae; on middle of inner surface every variation from no carina to distinct carina bearing beaded granules. Fingers sharp, stout.

Fifth leg.—Merus with spine larger than usual and length *c.* 2·5 times breadth; posterior border of propodus with 5–7 spines.

First male pleopod.—Short, stout, practically straight until tip which is sharply curved, flared, and truncated. Beyond basal lobes, both surfaces smooth. *Terminal bristles.*—On inner face 3–7 visible, and on outer face 15–20. On under surface inner and outer bristles joined into continuous series. All bristles short and stout, distal ones slightly the largest.

Colour.—After a few months in alcohol spots of bright orange-red on dorsal surface of carapace and especially along the ridges, and on tips of anterolateral teeth. Legs lightly spotted with sooty grey chromatophores, and a broad brown band running across middle of fingers, leaving pale areas both distally and proximally. After prolonged preservation, most specimens sooty brown.

Comments

Thalamita alcocki differs from the traditional description of *T. picta* only in possessing a relatively short basal antennal joint with a microscopically serrated keel. In this species, as in others, the ratio between length of the basal antennal joint and width of the orbit increases with the size of the specimen and *T. alcocki* thus falls into the synonymy.

At first sight, *T. gardineri* seemed distinct from *T. picta*, particularly as regards ornamentation of the chelipeds, but the Australian Museum series from Lord Howe I. form a complete link between the two. This is confirmed by the identical shapes of male abdomens and pleopods.

The variation in granulation of the basal antennal joint is perplexing and presumably due to wear, the typical structure being an unbroken ridge.

Small specimens approach *T. investigatoris*, which they resemble in having denticulated margins on the crest of the basal antennal joint, and in the indistinctness of the anterior mesobranchial ridge. The only clear distinguishing features appear to be the absence of costae and the reduction of spines on the upper surface of the hand. Apparently *T. investigatoris* is known only through the holotype ♂ and it seems possible that this may be an abnormal *T. picta*.

Distribution

From Mozambique and the Red Sea in the west to the Tuamotu Is. in the east (Balss 1938; Sakai 1939; Holthuis 1953). Sakai (1939) lists "Australia" in his distributional data, and although the species is widespread off the east coast, the source of Sakai's data has not been discovered.

Thalamita prymna (Herbst)

Figs. 2*R*, 3*R*; Plate 4, Fig. 3; Plates 8*L*, 9*E*

Cancer prymna Herbst, 1803, pp. 41–2, pl. LVII, fig. 2.
Thalamita prymna Milne Edwards, H., 1834, p. 461. Milne Edwards, A., 1861, pp. 360–1, 367. De Man, 1887, pp. 75–6, pl. IV, figs. 5, 6. Alcock, 1899, pp. 78–9 (lit. and synon.). Nobili, 1906*a*, pp. 201, 203–5. Stebbing, 1910, p. 310. Parisi, 1916, p. 176. Balss, 1922, p. 112. Yokoya, 1933, p. 178. Boone, 1934, p. 73, pl. 31–4. Sakai, 1934, p. 303; 1936, p. 131, pl. 40, fig. 1; 1939, pp. 413, 416, pl. LI, fig. 1. Shen, 1937, p. 133, fig. 18. Ward, 1942, p. 81. Barnard, 1950, pp. 174–5.
Thalamita prymna '*a*' Calman, 1900, p. 22.
Thalamita prymna var. *annectans* Laurie, 1906, pp. 418–19.
Thalamita stimpsoni McNeill, 1926, p. 307.
Thalamita prymna var. *pelsarti* Montgomery, 1931, pp. 427–9, pl. 24, fig. 2, pl. 28, figs. 3, 3*a*.
Thalamita prymna forms '*a*' and '*b*' Tweedie, 1950, pp. 84–6, fig. 1.

Material Examined

24 ♂♂ (9–72 mm); 10 ♀♀ (25–50 mm). Smallest ovigerous ♀ 41 mm; ovigerous ♀♀ from Sept.–Oct.; *Sacculina* infection, 3 per cent.

QUEENSLAND: Moa I. (Torres Str.), Murray I., Woody I., Low Isles, Orpheus I., Holbourne I. (Port Denison), Hope I., Hayman I., Bate Reef, Port Curtis, Heron I. NEW SOUTH WALES: Shellharbour. LORD HOWE I. NORTHERN TERRITORY: S. Shell I., Port Darwin.

Recorded habitats.—Reef flat, coral shingle; typically from coral localities.

Material illustrated.—Carapace, basal antennal joint, male abdomen: ♂ 60 mm, Low Isles (Qld. Mus. regd. No. W991 (part)). Male pleopod: ♂ 33 mm, Hope I., pres. Aug. 1913, A. R. McCulloch (Aust. Mus. regd. No. P3795).

Description

Front.—Six lobes, all protruding to same extent, giving front a flattened appearance. Submedians slightly the largest, followed by medians, then laterals (ratio of breadths of submedian frontal lobes against medians roughly 7 : 6 in present specimens, but in Calman's (1900) var. *c*, ratio stated as 3 : 2). Frontal lobes usually square-cut but occasionally rounded, especially laterals. Inner orbital lobes slightly arched and broad, approximately combined widths of submedian and lateral lobes.

Anterolateral teeth.—Five, first 3 large, 4th small or rudimentary, 5th smaller than 3rd.

Carapace.—Breadth *c.* 1·6 times length; usually smooth, or with hairs restricted to lateral and depressed portions. Usual ridges from frontals to epibranchials well developed but none behind epibranchials.

Basal antennal joint.—In adults, much wider than orbit (e.g. 1·58 times in ♂ 60 mm from Low Isles, in Qld. Mus.), but probably ranging to less than orbit (0·8) assuming that the 7 mm Murray I. specimen in Aust. Mus. is correctly identified. Crest bearing 3–5 conspicuous spines, typically 3–4. In 1 or 2 specimens, spines appear to have been worn down to tubercles.

Chelipeds.—Approximately equal, characterized by long, dark-tipped spines. Anterior border of arm bearing 3 stout spines, a 4th spinule near articulation of wrist. Wrist bears usual spines, all generally sharp. Two distinct carinae on outer surface of wrist, running to upper and lower spines respectively. Upper surface of wrist bears widely spaced rounded granules; similar granules line front margin of wrist and proximal portion of carina which leads to the elongate inner spine. Upper surface of wrist usually bears sparse felting of hairs. Hand with 2 or occasionally 3 spines on inner edge of upper surface, 2 very large and 3rd proximal spine either smaller or represented by a group of tubercles. Outer surface, in addition to a spine at the wrist articulation, bears the 2 usual spines, long and stout. Outer surface of hand bears 2 distinct carinae on lower surface of which uppermost, in larger specimens, is represented by row of rounded granules. A 3rd row of granules may be present and distinct; alternatively the upper half may show confused rows of granules. Inner surface either smooth with low but distinct carina or sparsely beset with large rounded granules, some forming a cariniform line. Under surface of hand typically smooth, but sometimes minutely granular, presumably in unworn specimens. In these, all surfaces except under surfaces bear a felting of hairs. Fingers long, sharp, and deeply grooved.

Fifth leg.—Merus slightly less than twice as long as broad, with usual spine; 9–13 spines on posterior border of propodus.

First male pleopod.—Elongate, tapering, and slightly sinuous, tip not expanded, and aperture oblique. Inner surface bears a few small bristles, beginning about four-fifths of the way up; on outer surface a row of *c.* 12 slender bristles which lead to

terminal armature of outer side. No terminal bristles on inner side, but on outer *c.* 7 short stout bristles, just behind tip, visible in profile view.

Colour, live specimen (Low Isles, 16.viii.54).—"Black areas behind frontal ridges, last two joints of fifth leg blue, tips of chelae purple" (W.S.). After alcohol preservation, tips of anterolateral teeth and cheliped spines dark brown.

Comments

The synonymy of this species has become extremely involved in the twentieth century, beginning with Calman (1900). Of his 3 forms, designated *Thalamita prymna a*, *b*, and *c*, *b* is treated under *T. stimpsoni*, while *c* is sufficiently different from the general concept of *T. prymna* possibly to be erected as a new species. His first form (*a*) is mainly characterized by the possession of 4 spines on the basal antennal joint, a very small but not rudimentary 4th anterolateral tooth, and 6 spines on the upper surface of the hand. It is evident from the published descriptions that the spinulation of the basal antennal joint can vary. Thus Barnard (1950) gives 1–3 spines, Milne Edwards (1861) 2–3 spines, and Sakai (1939) 3–4 spines; and 3–5 are visible in the present range of material. There are similar variations in the size of the 4th anterolateral tooth from "not so completely a rudiment" (Tweedie 1950) to rudimentary, and these again are found in the present specimens. In addition, the spinulation of the upper surface of the hand can vary between a total of 5–6 spines (i.e. 4–5 neglecting the spine at the wrist articulation). It is evident that Calman's form *a* merges into the general variability of the species.

Laurie (1906) erected the variety *annectans*, apparently mainly upon the continuance of the mesogastric ridge to the edge of the carapace. A similar feature is shown by Montgomery's (1931) var. *pelsarti* and by Tweedie's (1950) form *b*. In the present specimens a single individual shows this continuance, but is not otherwise noteworthy, and moreover there are specimens with scattered granules in this region which seem intermediate to those without trace of the continuance. Laurie's var. *annectans* is therefore included in the synonymy.

Montgomery (1931) erected 2 varieties of this species. Of these, his var. *proxima* is concluded to belong to *T. stimpsoni* and is discussed under that species. His var. *pelsarti* is distinguished by a variety of features most of which are certainly mere variations on the general pattern (e.g. nature of front, small 4th anterolateral tooth, and 6 spines on the upper surface of the hand). His other features (hairiness, and conspicuous granulation of the cheliped) might well be due to a relative absence of wear and tear.

Tweedie (1950) distinguished two forms, *a* and *b*, with the former, for example, having rounded frontal lobes, relatively larger 4th anterolateral teeth, the mesogastric ridge not continued to the edge of the carapace, considerable general hairiness, and granulated chelipeds. Once again, most of these features are probably due to absence of wear and moreover, specimens in the present collection serve as connecting links between the 2 forms.

This species is close to *T. coeruleipes* and *T. spinimana*. The occasional specimens with worn-down spines on the basal antennal joint probably key out as *T. stimpsoni*, from which the present species differs most obviously in having black-tipped spines on the chelipeds, and also in the shape of the inner orbital lobes.

Distribution

Published and present records within Australia are from Queensland (Calman 1900; McNeill 1926; Boone 1934), New South Wales, Western Australia (Montgomery 1931), and Northern Territory. Whitelegge's (1900) record from Norah Heads (33° 15′ S.) is suspect, and the recordings by Milne Edwards (1834), Hess (1865), Haswell (1882), and Henderson (1893) are not sufficiently localized for detailed consideration.

From Delagoa Bay and the Red Sea in the west to Japan and the Marshall Is. in the east (Milne Edwards 1861; de Man 1887; Ortmann 1894; Rathbun 1910*a*, 1911; Sakai 1939; Barnard 1950; Holthuis 1953).

Thalamita quadrilobata Miers

Figs. 2*G*, 3*G*; Plate 4, Fig. 4; Plates 8*M*, 9*F*

Thalamita quadrilobata Miers, 1884, pp. 539–40, pl. XLVIII, fig. *B*, *b*. Alcock, 1899, pp. 84–5.
Thalamita admeta var. *E intermedia* Borradaile, 1902, pp. 202–3.
Thalamita admeta var. *F quadrilobata* Borradaile, 1902, pp. 202–3.

Material Examined

QUEENSLAND: At Aust. Mus.: ♂ 15 mm, dredged in lagoon, Lady Musgrave I., Bunker Grp., 1926, M. Ward (regd. No. P12528); ♂ 19 mm, Torres Str., Sept.–Oct. 1928, M. Ward (regd. No. P12763). Ovigerous ♀ 24 mm, coral reef flat, Green I., near Cairns, Apr.–May 1953, F. A. McNeill and J. K. Howard.

Material illustrated.—Carapace: ♀ 24 mm. Basal antennal joint, male abdomen, male pleopod: ♂ 19 mm.

Description

Front.—Two lobes, separated by deep cleft, each lobe markedly concave on anterior border; inner orbital lobes little arched and three-quarters as wide as frontal lobes.

Anterolateral teeth.—Five, all sharp, 1st largest, 4th distinctly smallest.

Carapace.—Breadth *c.* 1·6 times length; 3 pairs of ridges on gastric region, with short median space between mesogastrics; epibranchial interrupted by cervical grooves, and also medianly; the 2 broad cardiacs with narrow median interruption; on each mesobranchial region a single short ridge, markedly elevated and very conspicuous. Entire surface, apart from ridges, covered with short hairs, removal of which reveals fine punctations, with very occasional low flattened wart. Postero-lateral extremity obtusely angled.

Basal antennal joint.—1½ times diameter of orbit and bearing crest with 3 major spines (a smaller 4th proximal spine on left side on 1 specimen).

Chelipeds.—Arm with 3 major spines on anterior border and a 4th smaller proximal spine; wrist spinulation normal, upper and lower outer spines terminating in smooth, flattened ridges. Area between these ridges covered with large granules. Upper surface of hand bearing 4 spines in addition to that present at wrist articulation (outer 2 spines on left hand often reduced by abrasion); outer surface with 3 ridges, each composed of conspicuous bead-like granules, lowest ridge continuing without

beading to end of immovable finger, and above it another unbeaded ridge running along length of finger only. Inner surface bears a central longitudinal granular ridge, and beneath it finer granules also arranged longitudinally. Under surface bears small pits superimposed upon minute squamiform markings. Movable finger like the immovable one, long and sharp, bearing 3 sharp keels on outer surface and 2 more rounded ones on inner surface.

Fifth leg.—Posterior border of merus finely serrated, bearing a conspicuous spine; propodus dentate on posterior border and bearing 8 irregularly spaced teeth.

First male pleopod (description based on single specimen).—Short, stout, slightly curved; tip apparently damaged. Beyond basal lobes, inner surface with sparse row of hairs, followed by regularly arranged short stout curved hairs. *Terminal bristles on inner side.*—Four, very long and stout, followed by 2 hairs. The 2 proximal bristles are the longest, and converge; the penultimate one is the shortest. *Terminal bristles on outer side.*—Fourteen; the most proximal at right angles to the appendage and slightly shorter than the next 4, which incline in a proximal direction. The 2 bristles at distal end short and thin, remaining 5 increasing in size progressively from tip.

Colour.—After 5 months in alcohol, tips of anterolateral teeth and spines of chelipeds reddish brown behind a pale extremity; fingers basally red with central dark brown band and pale tips; carapace with bright red spots sparsely distributed and mostly concentrated on the ridges; legs with incomplete bands of sooty grey.

Comments

The only divergence from Miers's (1884) description is the presence of 3 and not 2 spines on the outer surface of the wrist of the cheliped. In addition, Miers did not describe the red spots upon the carapace.

Alcock's (1899) comment that this is probably only a variety of *T. admete* is contradicted by the distinct difference in the basal antennal joint and first male pleopods. These are sufficiently significant to remove Borradaile's (1902) "*Thalamita admeta* var. *E intermedia*" well away from *T. admete* and close to the present species. The only apparent difference is that var. *E intermedia* has 2-lobed front, while *T. quadrilobata* supposedly has a 4-lobed front. However, the front is composed of 2 concave lobes and is more 2-lobed than 4-lobed. On this basis, Borradaile's variety is included in the synonymy.

Distribution

Seychelles, 4–12 fm (Miers 1884); Andaman Is. (Alcock 1899); Gilbert Is. (Holthuis 1953). Not previously recorded from Australia.

Thalamita sexlobata Miers

Figs. 2*B*, 3*B*; Plate 5, Fig. 1; Plates 8*N*, 10*K*

Thalamita sexlobata Miers, 1886, pp. 196–7, pl. XVI, fig. 2*a*, *b*, *c*. Henderson, 1893, pp. 373–4. Alcock, 1899, pp. 87–8. Stephensen, 1945, pp. 136–7, fig. 32*C*, *D*.
Thalamita sexlobata var. *plicatrifrons* de Man, 1902, pp. 651–3.
Thalamita poissonii Sakai, 1939, fig. 17.

Material Examined

9 ♂♂ (8–17 mm); 14 ♀♀ (8–17 mm). Smallest ovigerous ♀ 12 mm; ovigerous ♀ in December.

QUEENSLAND: N. Direction I., Peak Pt. near tip of C. York, Darnley I., Gatcombe Hd., Port Curtis.

Recorded habitats.—Dredged, 3–20 fm.

Material illustrated.—Carapace, basal antennal joint, male abdomen, male pleopod: ♂ 11 mm, dredged, 3–6 fm, off Peak Pt., near C. York, Sept. 1928, M. Ward (Aust. Mus. regd. No. P12642).

Description

Front.—Four-lobed and sinuous; median lobes slightly more than half width of laterals, projecting slightly beyond them; laterals broadly curved, with variable degree of indentation, such that some specimens almost approach a 6-lobed condition. Inner orbital lobes short and distinctly arched.

Anterolateral teeth.—Five, 1st distinctly largest, 4th smallest, sometimes rudimentary; 2nd and 3rd stout; 5th sharpest and slightly protruding.

Carapace.—Frontal ridges short and granular; protogastrics and mesogastrics clearly visible, latter being continuous across the mid line; epibranchial broadly interrupted at cervical groove; short pair of anterior mesobranchials and cardiacs well developed, median sometimes continuous and sometimes interrupted. Apart from ridges, carapace covered with short dense matting.

Basal antennal joint.—Much shorter than major diameter of orbit (*c.* 0·65–0·75), bearing a short, acute, raised, curved, granulated crest.

Chelipeds.—Right cheliped much stouter than left. Anterior border of arm bears 3 (occasionally 2) spines. Wrist bears 4 usual spines, innermost unusually well developed. Chelipeds as a whole bearing squamiform markings which show through a fine down. Four usual spines on upper surface of hand are long, sharp, and well developed, except that outer distal one is reduced to a tubercle. Three well-developed carinae on outer surface of left palm, but uppermost one on right cheliped indistinct. Fingers sharp.

Fifth leg.—Merus bearing usual spine; posterior margin of propodus bearing hairs but no spines.

First male pleopod.—Short, stout, slightly sinuous, and with flared tip. Inner surface ornamented only with 3 minute widely spaced subterminal spinules; outer surface with row of regularly arranged elongate bristle-like hairs beginning as a row about half way up appendage, and merging with terminal bristles. A shorter row of hairs commences about three-quarters of the way up appendage, on upper surface, and swings over just behind tip to join lateral row. *Terminal bristles on outer side.*—Merging with subterminal bristles; numerous (*c.* 10), elongate, but becoming shorter and stouter towards tip.

Comments

Sakai's (1939) figure of the male pleopod of *T. poissonii* evidently refers to the present species.

Distribution

Tongataba (Miers 1886); Tuticorin (Henderson 1893); Andaman Is., Persian Gulf (Alcock 1899); Gulf of Manaar (Laurie 1906); now Australia.

THALAMITA SIMA H. Milne Edwards

Figs. 2*C*, 3*C*; Plate 5, Fig. 2; Plates 8*O*, 9*G*

Thalamita sima Milne Edwards, H., 1834, p. 460. Milne Edwards, A., 1861, pp. 359, 367. Miers, 1876, p. 28; 1884, p. 231. Alcock, 1899, pp. 81–2 (lit. and synon.). Calman, 1900, p. 23. Borradaile, 1902, p. 201. Stimpson, 1907, pp. 83–4, pl. XI, fig. 2. Parisi, 1916, p. 176. Balss, 1922, p. 359. Hale, 1927, p. 151. Montgomery, 1931, pp. 430–1. Shen, 1934, p. 54, figs. 17, 18. Sakai, 1934, p. 304; 1936, p. 132, pl. 40, fig. 3; 1939, pp. 414, 423, fig. 16*a*, *b*, *c*, pl. LI, fig. 3. Stephensen, 1945, pp. 126–8, fig. 27*A–G*. Barnard, 1950, pp. 175–6, fig. 33*b*. Edmondson, 1954, p. 258, fig. 32*e–h*.

Portunus (*Thalamita*) *arcuata* de Haan, 1850, p. 43, pl. II, fig. 2.

Material Examined

88 ♂♂ (7–85 mm); 53 ♀♀ (9–53 mm). Smallest ovigerous ♀ 16 mm; ovigerous ♀♀ from Apr.–May, July–Sept., Nov.; *Sacculina* infection, 4·5 per cent.

QUEENSLAND: Mappoon, Possession I. (Endeavour Channel), Badu I., C. York, Peak Pt. near tip of C. York, Albany Passage, N. Direction I., Two Is., Eagle I., Holbourne I. (Port Denison), Bowen, Lindeman I., Shoal Pt. (Mackay), Cannonvale, Gatcombe Hd., Port Curtis, Fraser I., Caloundra, Moreton Bay (Redcliffe, Woody Pt. Pier, Pt. Lookout, Myora Banks, Mud I., Pat's Pt., Rainbow Channel, Cowan Cowan, Southport). NEW SOUTH WALES: Nelson's Bay (Port Stephens), Port Jackson, Botany Bay. WESTERN AUSTRALIA: Exmouth Gulf, Abrolhos, Roebuck Bay, Broome, Ninety Mile Beach, Cottesloe, Swan River, Garden I. NORTHERN TERRITORY: Port Darwin, Bathurst.

Recorded habitats.—Trawled and dredged, 2½–19 fm; intertidal and under stones, rocks, and amongst mussel clumps, low water springs; intertidal muddy flats.

Material illustrated.—Carapace, basal antennal joint, male abdomen, male pleopod: ♂ 44 mm, 3½ miles S. Woody Pt. Pier, Moreton Bay, 26.x.52, coll. E. M. Grant (Zool. Dept., Univ. Qld.).

Description

Front.—Not strongly arched; 2 lobes, separated by small but distinct cleft; inner orbital lobes slightly arched and 0·6 breadth of frontal lobes.

Anterolateral teeth.—Five, 1st much the broadest and bluntest, 4th smallest, 5th the most protruding. In very small specimens 4th tooth is minute.

Carapace.—Breadth *c.* 1·6 times length; ridges normal, mesogastric uninterrupted centrally and running sinuous course, epibranchial broadly interrupted at cervical, cardiac which is interrupted medianly often differing from remainder in being without granules. Entire carapace, apart from ridges, densely covered with short hairs, beneath which surface is smooth apart from minute pitting. Posterolateral angles obtusely rounded.

Basal antennal joint.—In smallest specimen, 21 mm broad, 1·06 times diameter of orbit, and in largest, 57 mm broad, 1·69 times. Bearing a smooth, markedly elevated, short, curved crest.

Chelipeds.—Subequal; excepting in very small specimens, majority of surfaces of joints covered with *large conspicuous squamiform tubercles separated by fine densely hirsute areas.* Anterior border of arm with a series of approximately 5 stout spines, decreasing in size proximally. Outer surface of wrist bears 3 low stout spines, often blunted to tubercles, outermost marking termination of a sinuous carina. Hand bearing 3 large spines on upper surface, 4th (on antero-external edge) reduced to blunt tubercle. No definite carinae on upper surface of hand; outer surface bears 3 carinae, upper 2 merging into squamiform markings, and lowermost, the most acute, continuing to tip of immovable finger. This bears in addition the usual shortish carina, lying above the last-named. Middle of inner surface of hand bears a broad low indistinct ridge, merging with squamiform markings, and from lower part of which a distinct carina runs to end of immovable finger. Under surface normally bears very conspicuous markings. A hirsute groove runs beneath immovable finger, almost to tip. Movable finger, like the immovable, long, slender, sharp, and deeply grooved.

Fifth leg.—Merus short, length $2\frac{1}{4}$ times breadth, and smooth posteriorly, except for large stout spine. Posterior border of propodus without spines, but with usual border of long stout hairs.

First male pleopod.—Curving and narrowing smoothly to widely flared tip. Outer surface bears spinules from base to mergence with terminal armature. This consists of spines increasing progressively in length, stoutness, and density to form a confused clump just behind flared tip and continuing on to under side of flared region. Behind this region, the bristles also spread to upper surface. Outer surface without armature, up to terminal bristles which are short, stout, and densely packed on flared portion. These bristles become shorter and stouter towards tip, and eventually become short stout spikes. In small specimens terminal bristling only is present, following same pattern as in larger, but with fewer bristles in both inner and outer clusters.

Colour.—After prolonged alcohol preservation, colour reduced to dark tips of anterolateral teeth and spines of chelipeds. Teeth on movable fingers are dark greyish brown, the colour spreading across fingers themselves close to tips, but leaving tips uncoloured. Upper surface of movable finger bright reddish brown proximally, becoming paler distally.

Comments

One large ♂ (Aust. Mus. regd. No. P11774) is abnormal in having left frontal region bilobed and this is apparently not due to accidental damage.

In the smaller specimens examined, the 4th anterolateral tooth is extremely small, the squamiform markings of the chelipeds are feebly developed, and the median frontal notch is indistinct. These specimens come very close to *T. poissoni.*

This species is an active swimmer near the bottom, and attempts to escape capture by swimming rather than burrowing.

Distribution

Published and present records within Australia are from Queensland (Tenison Woods 1881; Miers 1884, 1886; Ortmann 1894; Calman 1900; Grant and McCulloch 1906–7; Ward 1931), New South Wales (Miers 1884; Stead 1898; Ward 1937), South

Australia (Miers 1886; Hale 1927), Western Australia (Miers 1884; Rathbun 1924), and Northern Territory (Miers 1884).

In the west, from Mozambique to the Red Sea; and in the east, from Japan and Hawaii to New Zealand (see Miers 1894; Edmondson 1923, 1954; Sakai 1939; Barnard 1950).

THALAMITA SPINIMANA Dana

Figs. 2*O*, 3*O*; Plate 5, Fig. 3; Plate 8*P*, 9*H*

Thalamita spinimana Dana, 1852*a*, p. 283, pl. 17, fig. 8; 1852*b*, p. 85. Milne Edwards, A., 1861, pp. 364, 367; 1873, p. 165, pl. IV, fig. 5. De Man, 1887, pp. 76–8, pl. IV, fig. 7. Lanchester, 1900, p. 749. Sakai, 1936, p. 162, pl. XII, fig. 1. Shen, 1937, p. 131, fig. 17.

Material Examined

QUEENSLAND: ♀ 47 mm, ♂ 66 mm,* C. York, 1884 (Qld. Mus.); ♂ 44 mm, Goode I., Torres Str., 8.ii.32, M. Ward (Aust. Mus. regd. No. P10420).

Material illustrated.—Starred specimen.

Description

Front.—Six lobes, all protruding to same extent; submedians equal to or slightly wider than medians, both somewhat square-cut; laterals rounded, about two-thirds breadth of submedians. Inner orbital lobes markedly arched.

Anterolateral teeth.—Five, subequal, decreasing in stoutness and increasing in sharpness from front to rear; all black-tipped in spirit-preserved specimens.

Carapace.—Breadth *c.* 1·6 times length; usually smooth or hairs restricted to lateral and depressed portions. All usual ridges from frontals to epibranchials well developed, but none behind epibranchials.

Basal antennal joint.—Much wider than diameter of orbit (1·58 times in ♀ 47 mm, in Qld. Mus.), with elevated crest bearing cluster of either 2 or 3 spines and a single lower spine.

Chelipeds.—Approximately equal, characterized by long, dark-tipped spines and granules on upper surfaces. Anterior border of arm with either 3 or 4 stout spines, and a 4th spinule near wrist articulation. Wrist with usual long inner, and 3 smaller outer spines, and in addition, 2 small spines or spiniform granules on upper surface, 1 being on granulated carina leading to long inner spine. Inner side of upper surface of hand bears typically 4 long, sharp, black-tipped spines, except that most distal may be reduced to a blunt or barely recognizable tubercle. Outer surface bears the 2 usual spines and 1 at wrist articulation. Outer surface of hand bears 2 distinct granulated carinae, and on its upper surface, rows of granules of variable distinctness. Inner surface bears either a distinct longitudinal band of granules or 3 indistinct rows followed by widely spaced granules. Under surface varying from smooth to granular, presumably depending on wear; when granular, inner surface has a squamiform appearance. Fingers sharp and deeply grooved.

Fifth leg.—Merus less than twice as long as broad (*c.* 1·8 times), with usual spine; 10–12 spines on posterior border of propodus.

First male pleopod.—During permanent preparation this is liable to twist and to lose bristles; description is based upon a single *left* pleopod.

Elongate, thin, gradually tapering to fine tip, and with oblique aperture. Inner surface with double row of regularly spaced bristles from about one-third of the way up from the base to subterminal area, becoming longer distally. Here a short "tuft" shows in lateral view. Outer surface with a double row of elongate bristles, beginning about half way up the appendage and continuous with terminal armature, such that *c.* 40 bristles are visible in profile view. They become shorter and stouter distally, the last pair almost papilliform.

Comments

This species is close to the somewhat variable *Thalamita prymna*, but distinguished by its large 4th anterolateral tooth and by extra spines on the chelipeds. It is close to *T. coeruleipes*, being distinguished by the spines on the cheliped, by its broader carapace, and by the 1st male pleopods.

Distribution

Viti Archipelago, Pacific Ocean (Milne Edwards 1861); Singapore, New Caledonia, Palao, Malay Archipelago (Shen 1937); "Insel Nord Watchter" (possibly Amboina) (de Man 1887). Not previously recorded from Australia.

THALAMITA SQUAMOSA, sp. nov.

Figs. 2*K*, 3*K*; Plate 5, Fig. 4; Plates 8*Q*, 10*J*

Material Examined

QUEENSLAND: At Aust. Mus., Great Barrier Reef Exped. Collections, labelled in writing of F. A. McNeill—"no locality available, no doubt dredged": 3 ♂♂, 6 ♀♀, as follows: holotype (A) ♂ 10 mm, allotype (B) ♀ 8 mm, paratype (C) ♂ 9 mm, paratype (D) ♂ 9 mm, paratype (E) ♀ 12 mm, paratype (F) ♀ 9 mm, paratype (G) ♀ 10 mm, paratype (H) ♀ 7 mm, paratype (I) ♀ 7 mm. In addition, fragmented legs from the above material are designated J.

Material illustrated.—Carapace, male pleopod: specimen A. Basal antennal joint, male abdomen: specimen D.

Description

Front.—Four lobes, medians rounded, slightly protruding, separated by shallow indentations from lateral lobes which are 1·5–1·8 times as broad; lateral lobes with slightly concave anterior surface. Inner orbital lobes slightly arched and short, almost exactly equal to width of median frontal lobes.

Anterolateral teeth.—Four, all sharp, with 1st much the largest, 4th smallest, 2nd and 4th subequal.

Carapace.—Reasonably elongate, breadth *c.* 1·45 times length. The following ridges present: frontals, short but extremely elevated; protogastric short; mesogastric; epibranchial, interrupted only by cervical grooves; mesobranchial a single short ridge; and broad lateral cardiac ridges almost meeting or completely meeting in mid line. Carapace densely covered with fine feathered hairs, giving a slightly shaggy appearance.

Basal antennal joint.—Less than major diameter of orbit (0·74–0·91 in above specimens), carrying short crest edged with coarse rounded granules.

Chelipeds.—Right normally slightly larger than left (in specimens A, B, and H; the reverse in specimen F). All major surfaces covered with squamiform granules with intervening depressions bearing lines of hairs, reminiscent of *T. sima*. Anterior border of arm bears 3 spines and numerous smaller tubercles. Usual spine present at antero-external angle of wrist, the 3 usual spines on its outer surface sharp and conspicuous. Upper surface of hand bearing 4 spines in addition to 1 near wrist articulation, all stout but respective carinae ill-developed. Outer and inner surfaces of hand without carinae, except from those associated with immovable finger and for traces of 2 carinae on outer surfaces, especially in smaller specimens. These 2 surfaces show squamiform markings particularly clearly; they are also present but sometimes less distinct on under surface of hand.

Fifth leg.—Merus 2·7–3·3 times as long as broad, bearing usual posterior spine and having a characteristic narrowing in its distal third. Posterior border of propodus normally bears 3–7 spines, but in 2 legs examined these spines were absent.

First male pleopod.—Stout, short with an almost right-angle bend in middle, beyond which it is parallel-sided almost to tip. General surfaces bare, until just before tip. Inner surface with small almost triangular spinules beginning about two-thirds of the way up appendage and spreading into upper surface and also continuous with subterminal bristles. Here between 7 and 8 or 7 and 18 bristles are visible in profile view, with further series lying on upper surface of appendage. Outer side without bristles on the general surface, but with 4–5 bristles immediately behind tip.

Comments

This species is close to *T. hanseni* (Alcock 1899) but differs from it as follows:

(*a*) Crest of basal antennal joint is coarsely granular in the present species but smooth in *T. hanseni*.

(*b*) Merus of 5th legs is roughly 3 times as long as broad in the present species, as against "more than twice as long as broad" in *T. hanseni*.

(*c*) While the number of spines on the posterior border of the propodus of the 5th leg is variable, 5–7 are the most common numbers, as against 2 or 3 in *T. hanseni*.

(*d*) In the present species, 2nd and 4th anterolateral teeth are subequal, with 2nd slightly larger, whereas evidently the reverse applies in *T. hanseni*.

(*e*) All frontal lobes are deeply cut in *T. hanseni*, but only the median notch in *T. squamosa* is deep.

(*f*) The outer surface of the hand bears distinct squamiform markings in *T. squamosa*, but indistinct ones in *T. hanseni*.

(*g*) The outer frontal lobes of *T. squamosa* are characteristically shaped.

Thalamita stimpsoni A. Milne Edwards

Figs. 2*M*, 3*M*; Plate 6, Figs. 1–3; Plates 8*R*, 9*I*

Thalamita stimpsoni Milne Edwards, A., 1861, pp. 362, 367, pl. XXXV, fig. 4. Alcock, 1899, p. 79 (lit. and synon.). Nobili, 1906*a*, pp. 202, 205. Sakai, 1939, pp. 413, 416–17.
Thalamita prymna var. *stimpsoni* Borradaile, 1900, p. 579.
Thalamita prymna '*b*' Calman, 1900, pp. 22–3.

Thalamita prymna var. *proxima* Montgomery, 1931, pp. 429–30, pl. 24, fig. 1, pl. 29, figs. 1, 1*a*.

non *Thalamita stimpsoni* Sakai, 1934, p. 304 (=*T. prymna*).

Material Examined

54 ♂♂ (9–75 mm); 44 ♀♀ (18–63 mm). Smallest ovigerous ♀ 42 mm; ovigerous ♀♀ from months of Aug.–Oct.; *Sacculina* infection, 8 per cent.

QUEENSLAND: York I., Murray I., Badu I., C. York, C. Grenville, High I., Endeavour River, Low Isles, Palm I., Gould I., and Green I. (Family Grp.), Holbourne I. (Port Denison), Hope I., C. Upstart, Hamilton I., Lindeman I., Lupton Reef, Cannonvale, Bargara, Rat I. (Port Curtis), Capricorn Grp. (Heron I., Mast Head I., North West I., One Tree I., Tryon Reef), Pt. Cartwright, Moreton Bay (Caloundra, Myora, Dunwich, Goat I., Bird I.). NEW SOUTH WALES: Trial Bay, Yamba. WESTERN AUSTRALIA: Broome. NORTHERN TERRITORY: Darwin.

Recorded habitats.—Under stones, under mussel clumps and on mud flats, from low water neaps downwards; mainland and reef localities.

Material illustrated.—Carapace, basal antennal joint: ♂ 58 mm, Badu I., 26.vi.53, D. J. Tranter (Zool. Dept., Univ. Qld.). Male abdomen, male pleopod: ♂ 56 mm, Palm I., Townsville, 4.vii.56, coll. R. Bryson (Zool. Dept., Univ. Qld.). *T.* cf. *stimpsoni*, carapaces: ♂ 5 mm, Hope I., Qld. (Aust. Mus. regd. No. P3851); ♂ 14 mm, Saddleback I., Qld. (Aust. Mus. regd. No. P5319).

Description

Front.—Six lobes, all rounded and distinctly separated; medians slightly the broadest (in profile view), lying on lower plane than remainder; submedians with inner edges sloping gradually inwards; laterals distinctly the smallest. Inner orbital lobes broad, mostly straight, and slightly more than twice as long as median frontals.

Anterolateral teeth.—Five, all sharp, 1st stoutest, 4th smallest (less than half size of first 3), 5th slightly smaller than first 3.

Carapace.—Frontal ridges smooth, protogastrics with markedly serrated outlines, mesogastrics normally serrated or granular and barely interrupted in mid line; epibranchial interrupted by cervical grooves, and behind it smooth raised bars mark positions of 2 short mesobranchials and a broad median cardiac. Entire carapace, apart from ridges, densely covered with fine pile, removal of which reveals minutely shagreened appearance. Posterolateral extremity of carapace obtusely rounded.

Basal antennal joint.—Much wider than major diameter of orbit (1·6 times in 35 mm specimen to 2·1 in 56 mm specimen), bearing a crest composed of row of about 7 elevated rounded tubercles, typically broadly spaced but sometimes partly fused in pairs.

Chelipeds.—Right much stouter than left. Anterior border of arm bears 3 sharp spines and several small rounded tubercles. Wrist and hand spinulation normal. Upper surface of wrist bears patch of rounded tubercles. Outer surface of hand bears an indistinct upper, and distinct median and lower carinae, which in unworn specimens are bordered by rounded tubercles. Immovable finger bears lower carina continuous with lower one of hand and also upper shorter carina. Inner surface of hand bears

a median carina bordered by granules, and its lower surface bears vertical rows of tubercles. Lower surface of hand usually quite smooth, apart from groove along immovable finger, but in recently moulted specimens inner surface bears indistinct rows of tubercles while outer surface is hirsute. Apart from under surface of hand, and the various carinae, remainder of surfaces covered with bold rounded tubercles rising from amongst fine pile of hairs. Movable finger of larger cheliped stout and blunt, and of smaller cheliped more straight and slender.

Fifth leg.—Merus broad, approximately 1·85 times as long as broad, smooth posteriorly, except for usual spine; posterior border of propodus bearing 10–12 fine spines.

First male pleopod.—Gradually tapering and curved to rounded, pointed tip. On inner surface spinules begin about a quarter of the way from base, enlarge progressively, and become a double row of bristles which do not extend to terminal region, which is bare. The outer surface is without bristles up to terminals, of which *c.* 21 are visible in profile view. They are closely packed just behind tip, with longest ones, *c.* two-thirds width of tip, slightly behind end of clump.

Colour.—Five specimens from dark habitats have anterior to frontal ridge of carapace nearly black, a trefoil black mark in region of cervical grooves to median cardiac region, general surface bluish purple, mottled with very pale blue spots. From light habitats (e.g. coral reefs) specimens are pale with mottling.

Comments

Calman's (1900) *Thalamita prymna 'b'* does not seem to differ in any way from *T. stimpsoni*, and its possession of a granular basal antennal joint removes it from *T. prymna* as here designated. Montgomery's (1931) *T. prymna* var. *proxima* is for similar reasons removed from *T. prymna*. Its only difference from the present species is the presence of a band of granules separating the lower from the inner surfaces of the hand of the cheliped. In *T. stimpsoni* there are typically in this region a series of vertical rows of granules; but in some cases the vertical arrangement is less apparent, in which case a band is distinguishable. It should be noted that the ratios of lengths to breadths of the carapace in Montgomery's table (p. 429) do not agree with the proportions in his figure (Plate 24, Fig. 1), which latter agree with the ratio of breadth to length as defined in the present description.

Two small specimens of *Thalamita* in the Australian Museum collections (P3851 and P5319) are perplexing. Details of the first are: ♂ 6 mm, Hope I., Qld., pres. Aug. 1913, A. R. McCulloch. The carapace is distinctly long (breadth 1·2 times length); the inner orbital lobes are markedly curved; and the basal antennal joint which bears a granular crest is two-thirds the width of the orbit. Details of the second specimen are: ♂ (*Sacculina*-infected) 14 mm, Saddleback I., off Port Denison, pres. June 1921, E. H. Rainford. The carapace is of more normal dimensions (breadth 1·5 times length), and the inner orbital lobes are curved, but less so than in the first specimen. The basal antennal joint bears an obscurely granular crest which is *c.* 0·7 width of the orbit.

Neither of the above specimens agrees with any known species and both key into the *tenuipes*, *imparimana*, *wakensis*, *malaccensis* region. Originally it was thought that both were new species, but the differences between them are insufficient to

justify their separation from one another. Both have the general facies of *T. stimpsoni* and are separated from it only by:

(*a*) Shortness of the basal antennal joint; as shown earlier this is an unreliable feature.

(*b*) The curvature of the inner orbital lobes. This curvature decreased from the smaller to the larger specimen, and in a more normal-sized specimen a straight and extended orbital lobe could be expected. A similar elongation of an inner orbital lobe, but to a less marked degree, is apparently shown in *T. prymna*.

(*c*) The relative length of the carapace in the smaller specimen.

(*d*) The obscurity and irregularity in the granulation of the ridge on the basal antennal joint. It is tentatively concluded that both are juvenile specimens of *T. stimpsoni*.

This is probably the commonest and most ubiquitous species of the genus in south Queensland. At Low Isles, north Queensland, Anne Stephenson (1934) found that the species spawns throughout the year but especially in the warmer months from October to March.

Distribution

Published and present Australian records are from Queensland (Tenison Woods 1881; Haswell 1882; Miers 1884; Ortmann 1894; Calman 1900; Grant and McCulloch 1906–7; Johnston 1917; McNeill 1934; Stephenson *et al.* 1931; Stephenson 1934), New South Wales (Ward 1937), Lord Howe I. (McNeill 1934–7), Western Australia (Montgomery 1931), and Northern Territory (Miers 1884).

Wider distribution has been summarized by Sakai (1939) as: Asiatic coasts of Indian Ocean, East Indies, and West Pacific from Japan and Samoa to Lord Howe I. It has not been recorded from east Africa, where the closely related *T. danae* is present (Barnard 1950).

THALAMITA TRILINEATA, sp. nov.

Figs. 2*E*, 3*E*; Plate 6, Fig. 4; Plates 8*S*, 10*L*

Material Examined

QUEENSLAND: Holotype ♂ 11 mm, Murray I., Aug.–Oct. 1907, C. Hedley and A. R. McCulloch (Aust. Mus. regd. No. P2863).

Description

Front (right frontal region damaged).—Front sharply arched with inconspicuous median notch, and with broad median lobes separated by shallow notches from anterolaterally directed lateral lobes *c.* one-third as broad as the medians. Medians with inconspicuous interruptions at *c.* one-seventh of breadth from mid-point, probably representing remnants of a division into median and submedian frontal lobes. Inner orbital lobes short, as broad as lateral frontals, slightly arched.

Anterolateral teeth.—Four, the 4th of those normally present represented by a small granule; 1st much the stoutest and the last the sharpest and most protruding.

Carapace.—Long, breadth 1·4 times length. The 3 normal gastric ridges are present, with mesogastric unusually long (five-eighths of the carapace breadth at its level), and with no median interruption; epibranchial with neither median nor cervical interruptions; median cardiac also uninterrupted and noteworthy in extending to mesobranchial regions, occupying nearly three-quarters of carapace breadth at its level. Apart from ridges, carapace somewhat sparsely covered with long hairs, removal of which reveals microscopic granulation.

Basal antennal joint.—Slightly shorter than major diameter of orbit (0·9), bearing an acute ridge whose edge is formed of *c.* 15 fused rounded granules.

Chelipeds.—Slender, left slightly larger than right, most surfaces covered with long hairs overlying granulations. Arm, wrist, and hand with usual spines. Outer surface of hand with 2 lower carinae distinct and formed of regular rows of granules, uppermost carina represented by broad irregular row of granules. Inner surface with a central carina composed of a slightly irregular granular row. Lower surface densely covered with rounded tubercles, mostly of a uniform small size. Fingers long and sharp.

Fifth leg.—Merus extremely long, $2\frac{3}{4}$ times as long as broad, posterior border of propodus bearing 5–6 spines.

First male pleopod (based on a single, possibly twisted specimen).—Short, slightly curved, the tip blunt, club-shaped, and slightly swollen. On the inner surface there are spinules which start about one-third of the way up and run up to the terminal armature; these visible only in a permanent preparation. *Terminal armature on the inner side.*—Consists of rows of stout bristles, which begin on upper surface and run obliquely forwards. Roughly 5 such rows of bristles are present, *c.* 4 bristles per row, and the rows continue to under surface, *c.* 20 bristles being visible in profile view. *Terminal bristles on outer side.*—Consist of very close-packed longitudinal patch or double row lying on upper surface and projecting sideways so that *c.* 25 are visible in profile view.

Colour.—After prolonged alcohol preservation, the only suggestion of pigmentation is of a broad bar of colour having crossed the fingers about two-thirds of the way to their distal extremity.

Comments

The discovery of this species makes the keying of the genus more than usually difficult. The front is almost exactly on the borderline between being recognizable as 4-lobed or 6-lobed.

As a 6-lobed form, the species keys with *T. picta,* which it also resembles in the form of its basal antennal joint (allowing for the modified description of *T. picta* as here given). It differs, however, in the form of the frontal lobes, and most conspicuously in possessing a very small 4th anterolateral tooth.

As a 4-lobed form, the species keys out with *T. wakensis* and *T. seurati.* It differs from *T. wakensis* in the form of the "median" frontal lobes, in the degree of conspicuousness of the cardiac ridge, and in the male pleopod. It differs from *T. seurati* in the form of the basal antennal joint, which in *T. seurati* is a conspicuous crest with sharp granules whereas in *T. trilineata* it is a conspicuous crest with rounded granules. The specific name is derived from the 3 conspicuous lines traversing the carapace.

III. Discussion

(*a*) *The Relationship of* Thalamita *to other Genera*

It has long been recognized that *Thalamita* is difficult to separate from *Charybdis* de Haan 1835 and from *Thalamonyx* A. Milne Edwards 1873. Thus Leene (1938) felt unable to give a satisfactory demarcation of the genus *Charybdis*, and repeated Alcock's (1899) definition. Alcock himself stated (p. 73): "Obviously different as the extremes are, the forms included under *Charybdis* (=*Goniosoma*) and *Thalamita* yet constitute an unbroken series and there is no one character, still less a combination of characters, by which the two groups can be sharply segregated". The only workable features separating the two genera are the relatively oblique anterolateral borders characteristic of *Charybdis* and the presence of six anterolateral teeth in *Charybdis* against five in *Thalamita*.

The obliqueness of the anterolateral borders, at best a relative feature, does not apply to such species as *T. sima* whose other features place it firmly in the genus *Thalamita*. Milne Edwards (1873) erected the genus *Thalamonyx* to include five-toothed forms with a *Charybdis*-like obliqueness to the anterolateral borders, giving as a second feature a two-lobed front. Many species of *Thalamita* have two-lobed fronts, and the present paper describes a new species (*T. annulipes*) with a *Charybdis*-like anterolateral obliqueness and a four-lobed front. There are two possibilities: either to retain the genus *Thalamonyx* on a single feature or to widen the definition of *Thalamonyx* to include species with four-lobed fronts. The former course appears more logical, and if so the type species of *Thalamonyx danae* A. Milne Edwards 1869 will need a new specific epithet, *danae* being preoccupied (Stimpson 1858). The name *Thalamita anomala* is suggested, unless *Thalamonyx danae* and *T. gracilipes* A. Milne Edwards 1873 are in fact synonymous as some authors have suggested (see Alcock 1899). If so the species would become *Thalamita gracilipes* (A. Milne Edwards). A widening of the generic definition of *Thalamita* is also required, and has been effected by insertion of "normally" into the second sentence of the present generic description.

The presence of five as against six anterolateral teeth appears to be an unequivocal feature separating *Thalamita* from *Charybdis*. However, there are five species of *Thalamita* (*T. exetastica*, *T. macrodonta*, *T. spinifera*, *T. macrospinifera*, and *T. macropus*) in which there is a tiny subsidiary tooth at the base of the first. There is also one species of *Charybdis* (*C. rathbuni* Leene 1938) in which the second tooth is very small. The distinction between a "tiny" tooth which is neglected and a "very small" tooth which is included appears to be altogether too slight to effect a meaningful generic separation.

Further examination of the six relevant species is required before a major upsetting of accepted names could be advocated. Of the six species, only *T. macropus* has been adequately examined, particularly with reference to the male pleopods, which are more like those of a typical *Charybdis* (see Leene 1938) than of a *Thalamita*.

Thalamitoides, erected by A. Milne Edwards (1869, pp. 146–7) as a subgenus of *Thalamita*, is in a different category. It is sufficiently distinctive for generic status, with diagnostic features as follows: spoon-shaped tips to chelipeds, very broad front, and extremely spinous hands to the chelipeds. No specimens of this genus have appeared in Australian collections.

(*b*) *Intrageneric Classification*

There have been attempts (e.g. Montgomery 1931) to erect somewhat informal species groups within the genus, and there are several groups of species whose general structure shows close resemblances, and which are reasonably distinct from the remainder. These are:

(i) A *prymna* group, comprising *T. prymna*, *T. crenata*, *T. coeruleipes*, *T. danae*, *T. spinimana*, and *T. stimpsoni*: large species with six-lobed fronts, entire first anterolateral teeth, and relatively long basal antennal joints.

(ii) An *exetastica* group, comprising *T. exetastica*, *T. macrodonta*, *T. macrospinifera*, *T. macropus*, and *T. spinifera*: with six-lobed fronts and with a tiny subsidiary tooth at the base of the first anterolateral tooth. As already discussed, this group is very close to, and possibly should be transferred to, the genus *Charybdis*.

(iii) A *chaptali* group, comprising *T. chaptali*, *T. parvidens*, and *T. poissoni*: with two-lobed fronts, steeply arched inner orbital lobes, and indistinct frontal notches.

(iv) An *admete* group, comprising *T. admete*, *T. auauensis*, *T. granosimana*, *T. integra*, *T. margaritimana*, *T. quadrilobata*, and *T. spiceri*: with two-lobed fronts, and relatively straight inner orbital lobes. *T. dakini* and *T. medipacifica*, which are probably synonyms, and have minute lateral lobes, also belong to this group.

Two points should be stressed:

(*a*) A large number of species remain outside these postulated species groups; and until the genus as a whole can be arranged in groups the present arrangement must be tentative.

(*b*) The groups are demarcated by general characters, excluding those of the first pleopods of the males.

Considering the male pleopods, there are five main types, suggesting five possible species groups, as follows:

(i) A *prymna* group, including *T. prymna*, *T. crenata*, *T. coeruleipes*, *T. danae*, *T. spinimana*, and *T. stimpsoni*: tip gradually tapering, aperture oblique, outer bristles pointing distally.

(ii) A *macropus* group, including *T. macropus* and *T. spinifera*: tip gradually tapering, aperture oblique, outer bristles (which are of normal size) almost at right angles to the appendage. On the basis of pleopod structure the group is close to the previous one, but probably even closer to parts of the genus *Charybdis*.

(iii) A *chaptali* group, including *T. chaptali*, *T. parvidens*, and *T. poissoni* (Stephensen 1945 non Sakai 1939): with tips turned over, and extremely stout bristles especially at one side of the appendage.

(iv) An *admete* group, including *T. admete*, *T. auauensis*, *T. integra*, *T. medipacifica*, and *T. quadrilobata*: with extremely stout bristles sticking out almost at right angles from both sides of the appendage.

Although these groups are smaller than those previously detailed, a reflection of the fact that male pleopods are unknown for many of the species, the similarities will be apparent.

Throughout the genus as a whole the structure of the smaller species approaches more closely to the juveniles than to the adults of the larger species: for example, in the relative shortness of the basal antennal joint and in the relative smallness of the fourth anterolateral tooth. Within the genus two possible evolutionary schemes could be postulated:

(1) That larger species have been the ancestral types from which the smaller have developed by precocious attainment of maturity. Supporting this idea is the fact that in general the larger species are also closer to the genus *Charybdis* than the smaller species.

(2) That smaller species have been the ancestral types from which larger species have been a later development. The smaller species, like the majority of Brachyura, are crevice dwellers, and apparently live in and only slightly modify their habitats. The larger species include the more active swimmers and burrowers which are more emancipated from the "basic crab habitat", and are thus likely to be a later evolutionary development.

(c) *The Biogeography of the Species in Australian Waters* (Fig. 5)

The Australian species can be divided biogeographically into groups:

(i) Those recorded effectively from single localities and for which there are, therefore, insufficient data for discussion. These comprise *T. annulipes*, *T. dakini*, *T. integra*, *T. spinimana*, *T. squamosa*, and *T. trilineata*.

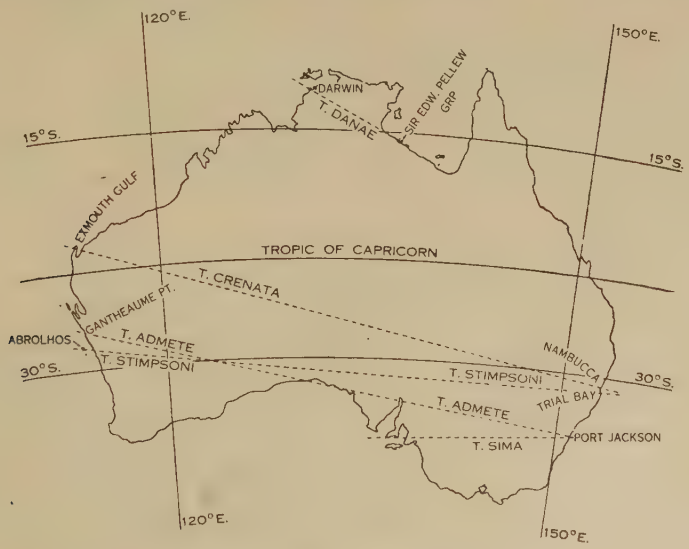

Fig. 5.—Southernmost limits of common species of *Thalamita*.

(ii) Those recorded only from the east coast. These comprise *T. chaptali*, *T. coeruleipes*, *T. cooperi*, *T. inhacae*, *T. picta*, *T. quadrilobata*, and *T. sexlobata*. The restriction is not due to a purely Pacific Ocean distribution of the species in question, all having been recorded from the Indian Ocean. It is possibly due to a marked

preference for localities on or near coral structures and the occurrence of three of them, *T. chaptali*, *T. inhacae*, and *T. picta*, from Lord Howe I. would seem to support this concept. It seems equally likely that the species also occur off the north-west coast of Australia but have not yet been collected therefrom.

(iii) Those recorded from both east and west coasts. These comprise:

(1) *T. prymna*, which occurs in the Great Barrier Reef area, at Lord Howe I., and on the west coast south to the Abrolhos. If Whitelegge's (1900) record is not accepted then the highest common factor appears to be the occurrence of coral-dominated habitats.

(2) A group consisting of *T. crenata*, *T. stimpsoni*, *T. admete*, and *T. sima*. These common species disappear progressively from north to south in the order listed, and apart from *T. sima* extend further south in the east than in the west. It seems probable that the southerly extension of these Indo–West Pacific species is limited by water temperature. Possibly the same factor limits *T. danae* to the Northern Territory.

(3) *T. macropus*, which occurs in the Abrolhos in Western Australia and again in New South Wales, but has not been recorded elsewhere. One can only postulate that this species previously extended from west to east across the south of Australia. Possibly it is still present on the southern coasts but has escaped collection, or more probably the originally continuous population has become two isolated "pockets".

(iv) *T. intermedia* is an anomalous case, being recorded from north-eastern, north-western, and southern Australia. Hale (personal communication) suggests the possibility of a mistaken locality for this last record.

The overall conclusion is that the Australian distribution of the species is very imperfectly known, and that more intensive collection in southern Australia and more especially along the north-western coast is required before any clear picture can be recognized.

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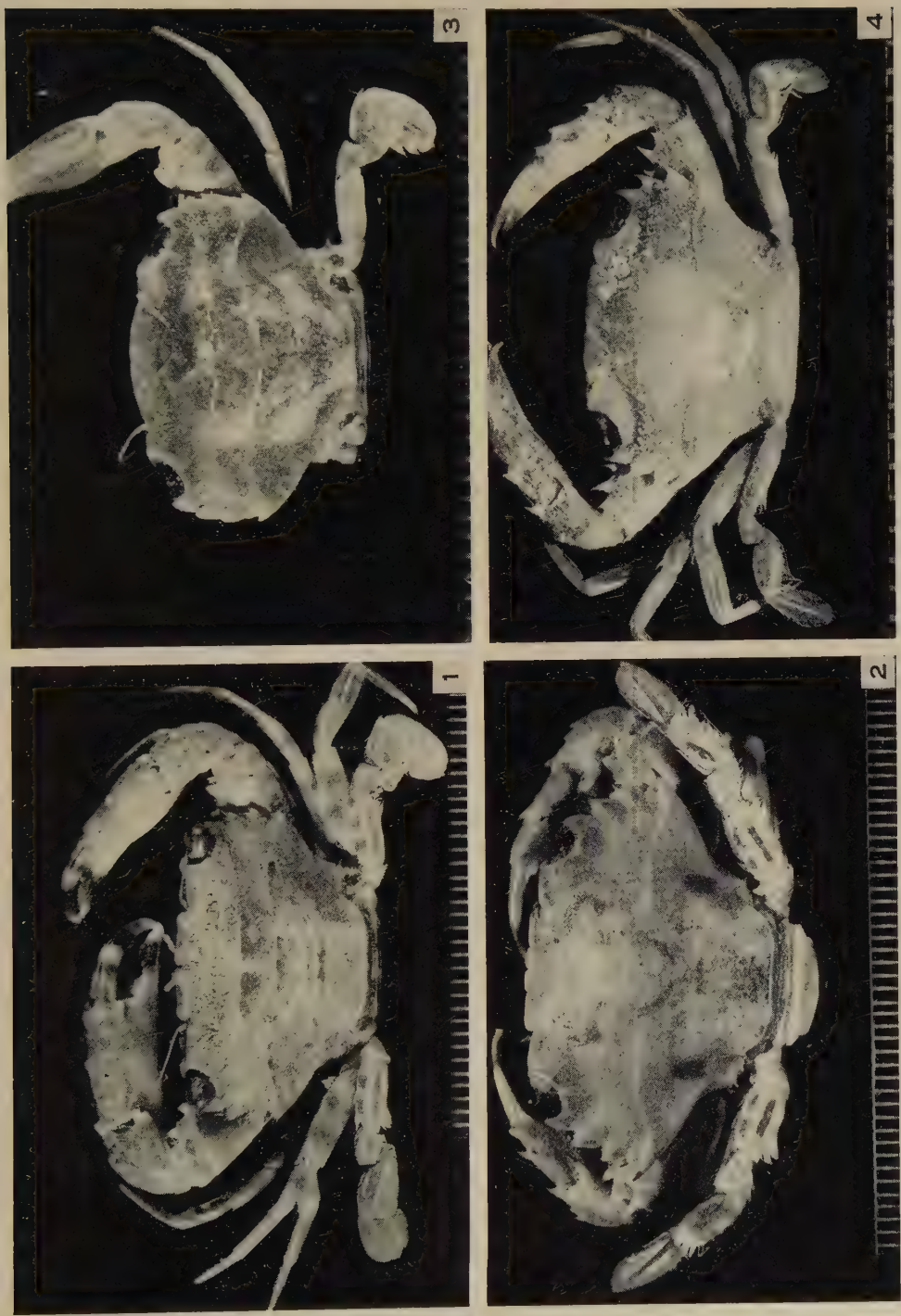
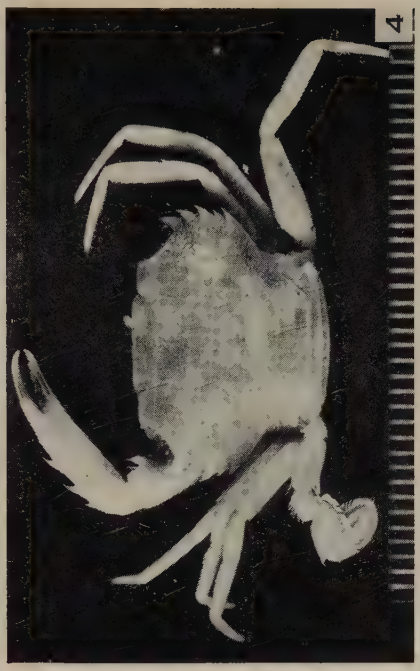


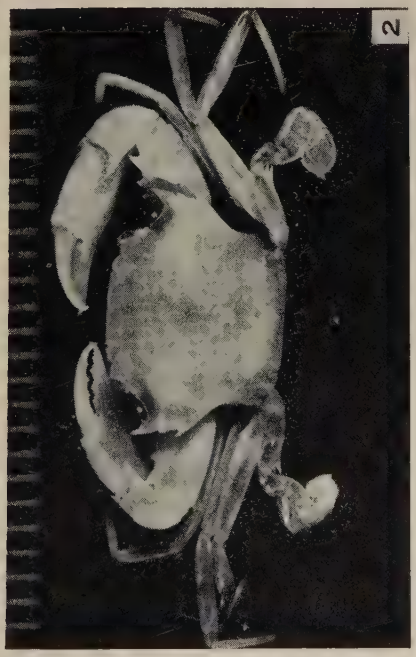
Dorsal views of *Thalamita* spp. Scale divisions, 1 mm. Fig. 1.—*T. admete*. Fig. 2.—*T. annulipes*. Fig. 3.—*T. chaptali*. Fig. 4.—*T. cooperi*.

AUSTRALIAN PORTUNIDS. I

Dorsal views of *Thalamita* spp. Scale divisions, 1 mm. Fig. 1.—*T. coeruleipes*. Fig. 2.—*T.* cf. *coeruleipes*. Fig. 3.—*T. crenata*; inset shows abnormal specimen with fused median and submedian frontal lobes. Fig. 4.—*T. dakini*.

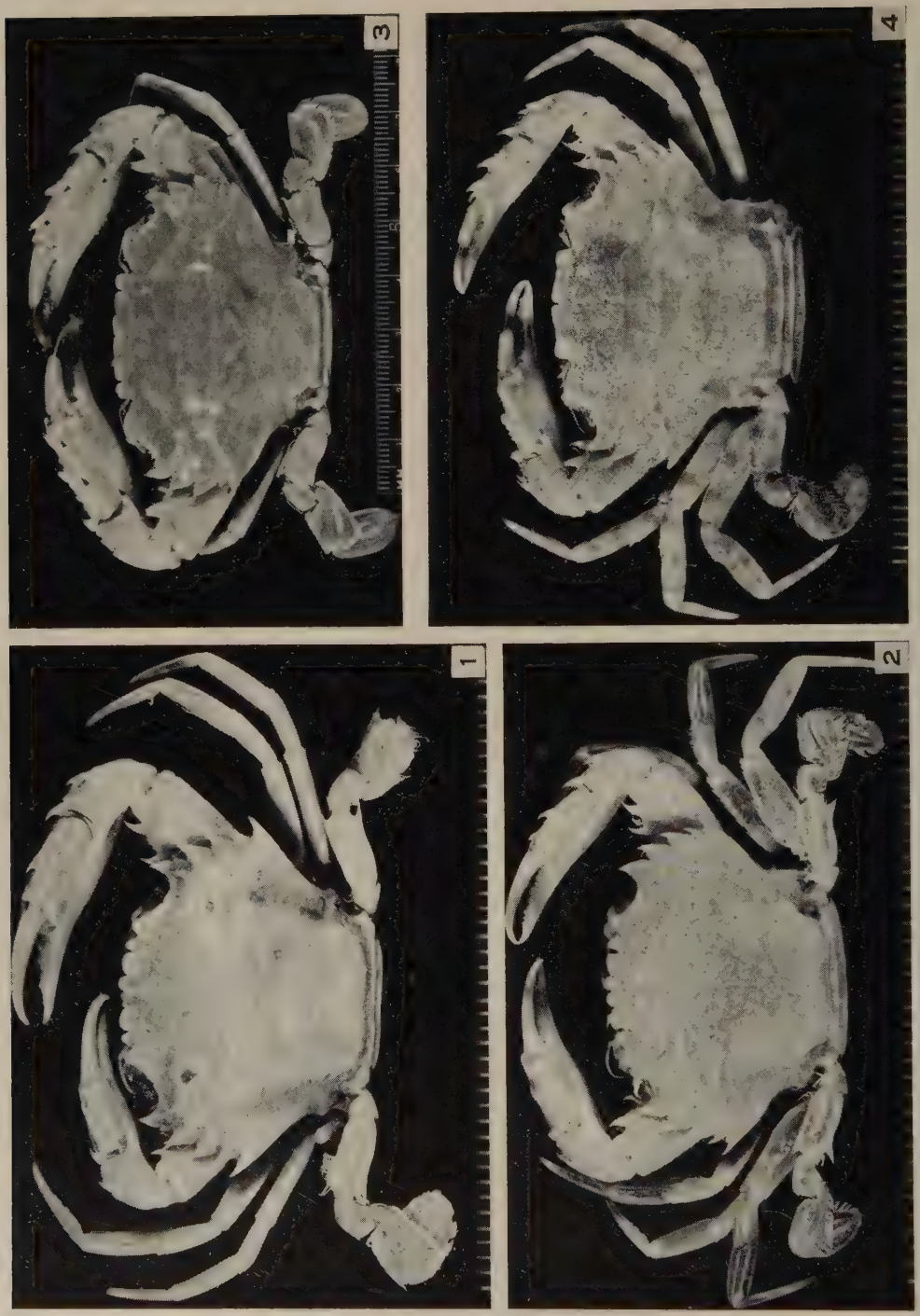
AUSTRALIAN PORTUNIDS. I





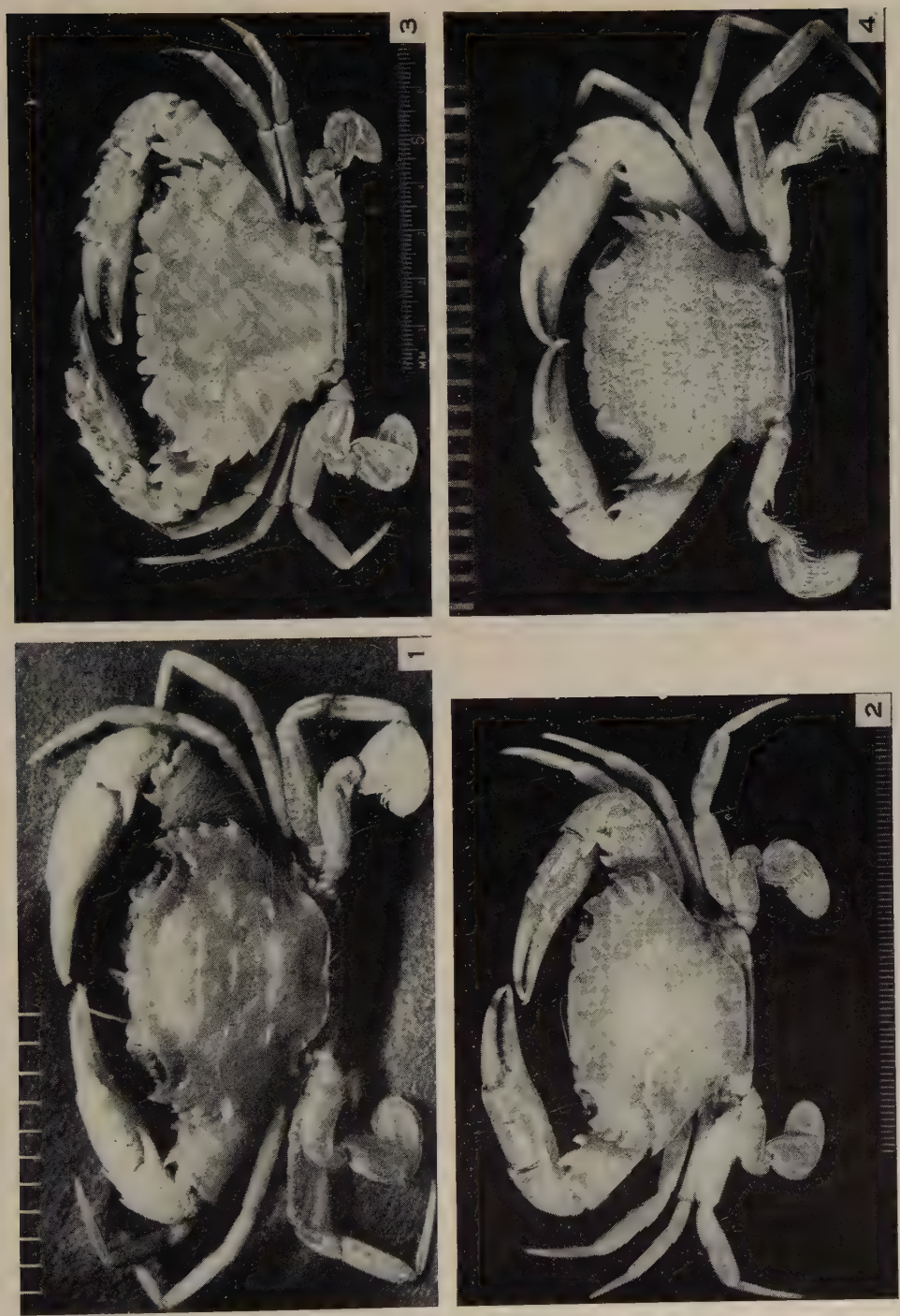
Dorsal views of *Thalamita* spp. Scale divisions, 1 mm. Fig. 1.—*T. danae.* Fig. 2.—*T. inhacae.* Fig. 3.—*T. integra.* Fig. 4.—*T. intermedia.*

AUSTRALIAN PORTUNIDS. I



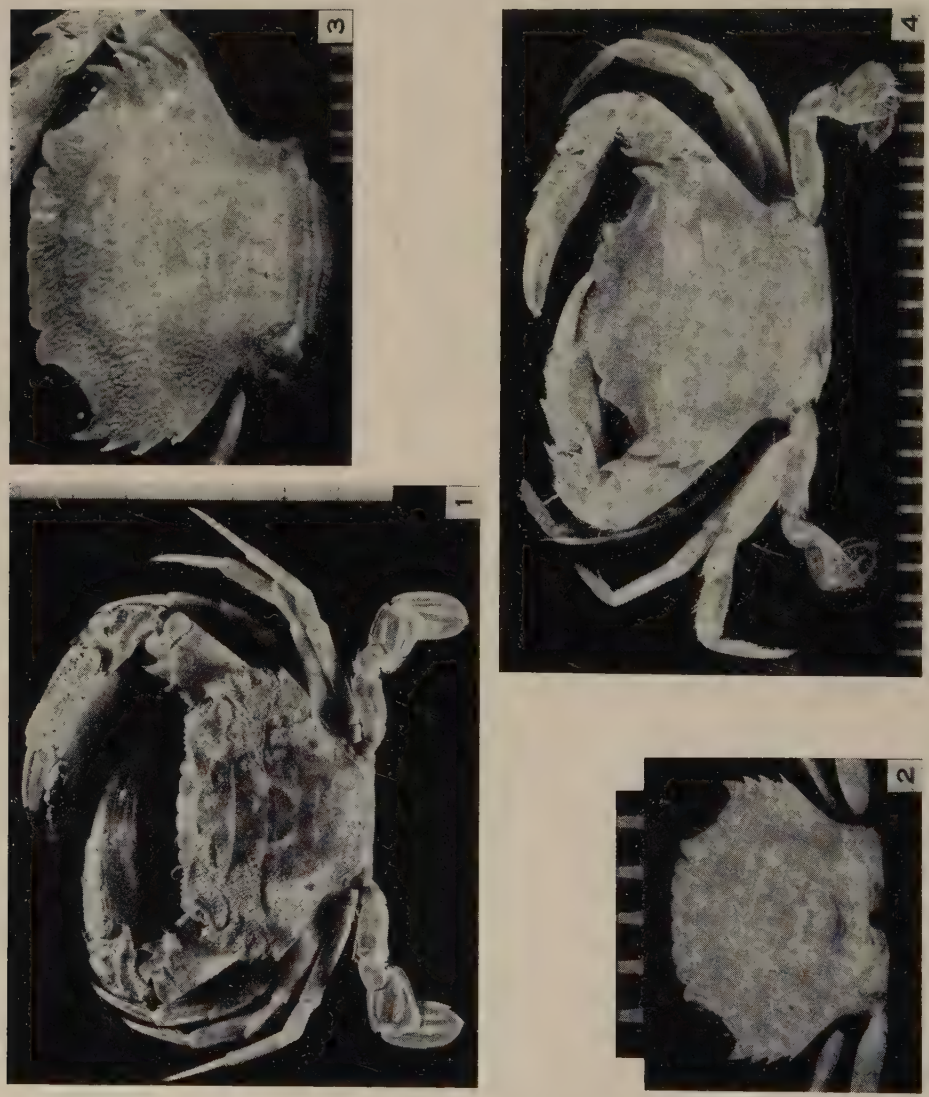
Dorsal views of *Thalamita* spp. Scale divisions, 1 mm. Fig. 1.—*T. macropus*. Fig. 2.—*T. picta*. Fig. 3.—*T. prymna*. Fig. 4.—*T. quadrilobata*.

AUSTRALIAN PORTUNIDS. I



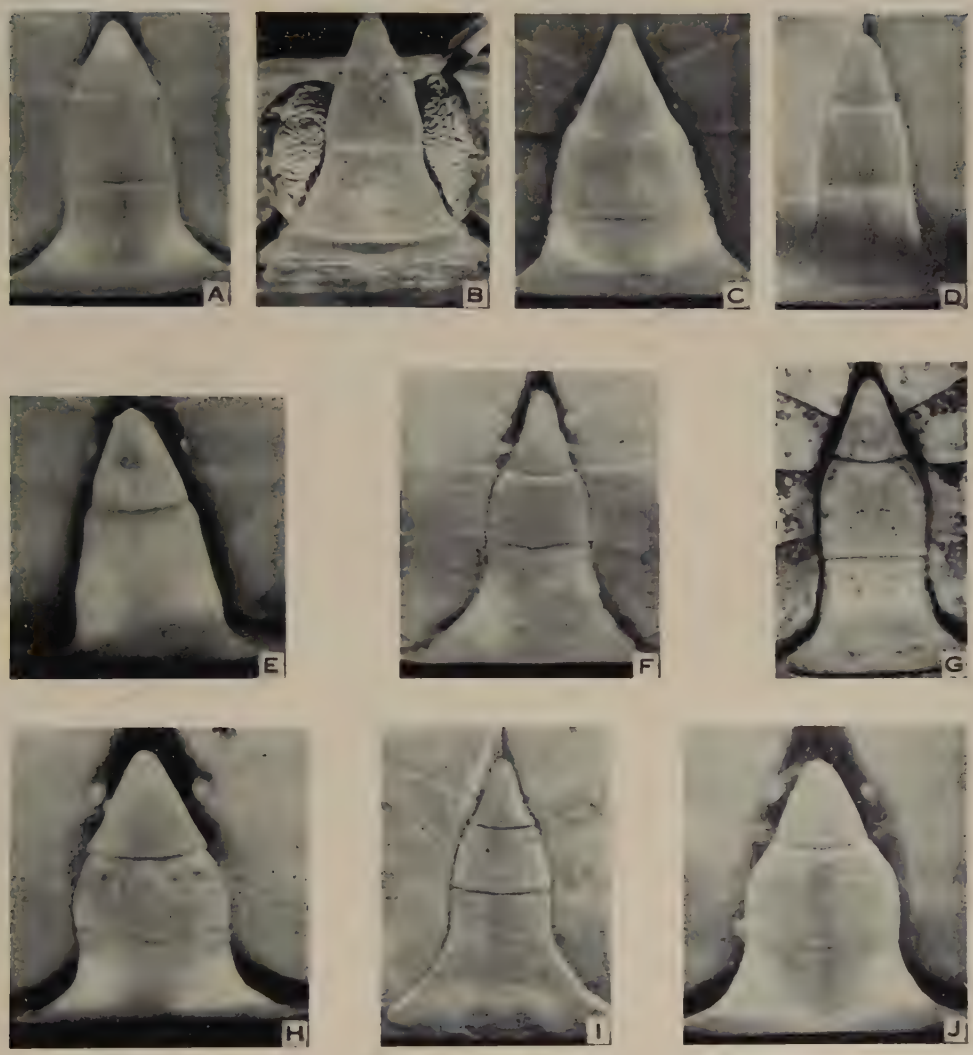
Dorsal views of *Thalamita* spp. Scale divisions, 1 mm. Fig. 1.—*T. sexlobata*. Fig. 2.—*T. sima*. Fig. 3.—*T. spinimana*. Fig. 4.—*T. squamosa*.

AUSTRALIAN PORTUNIDS. I



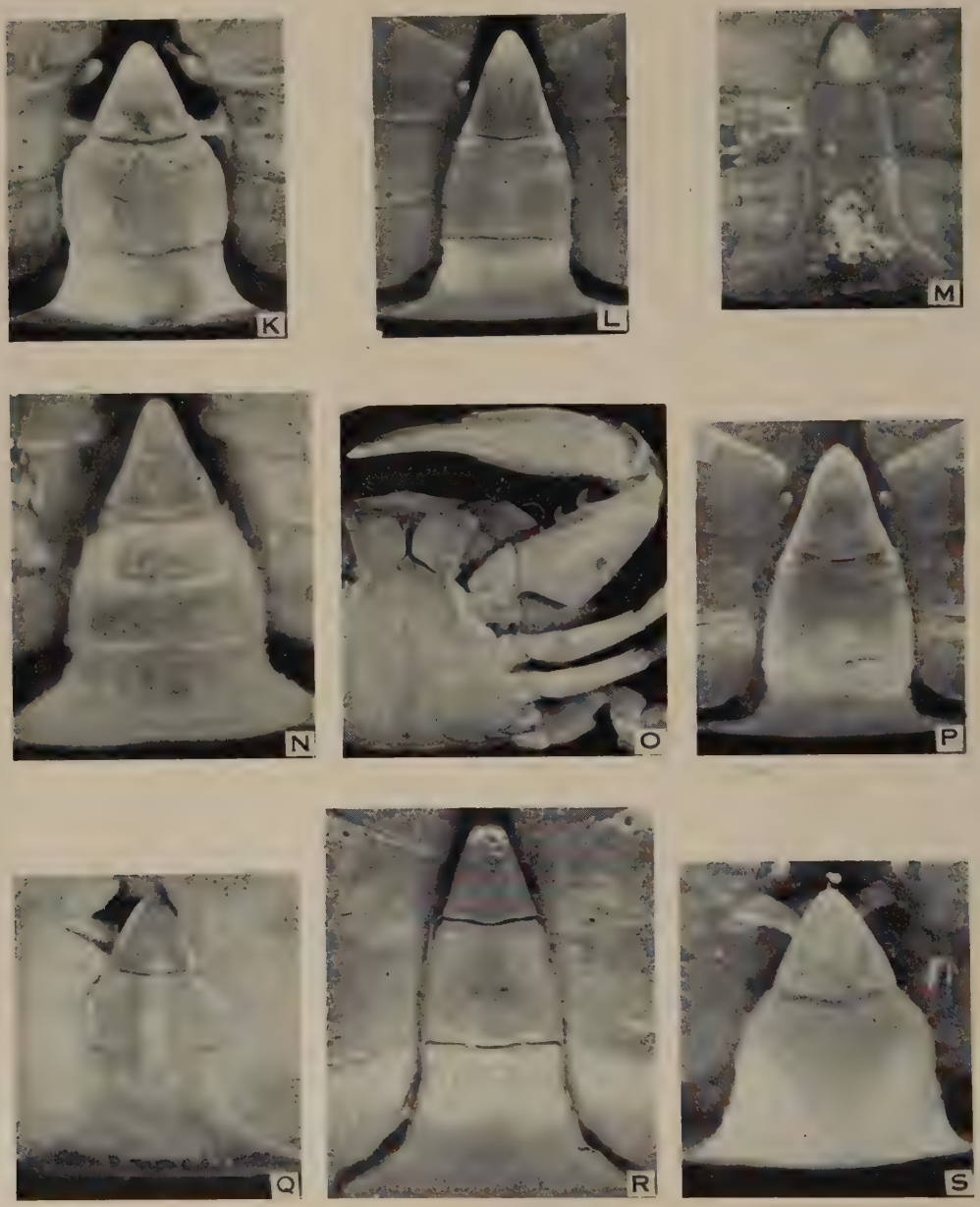
Dorsal views of *Thalamita* spp. Scale divisions Fig. 1, 1 cm, Figs. 2–4, 1 mm. Fig. 1.—*T. stimpsoni*. Figs. 2, 3.—*T.* cf. *stimpsoni*. Fig. 4.—*T. trilineata*.

AUSTRALIAN PORTUNIDS. I



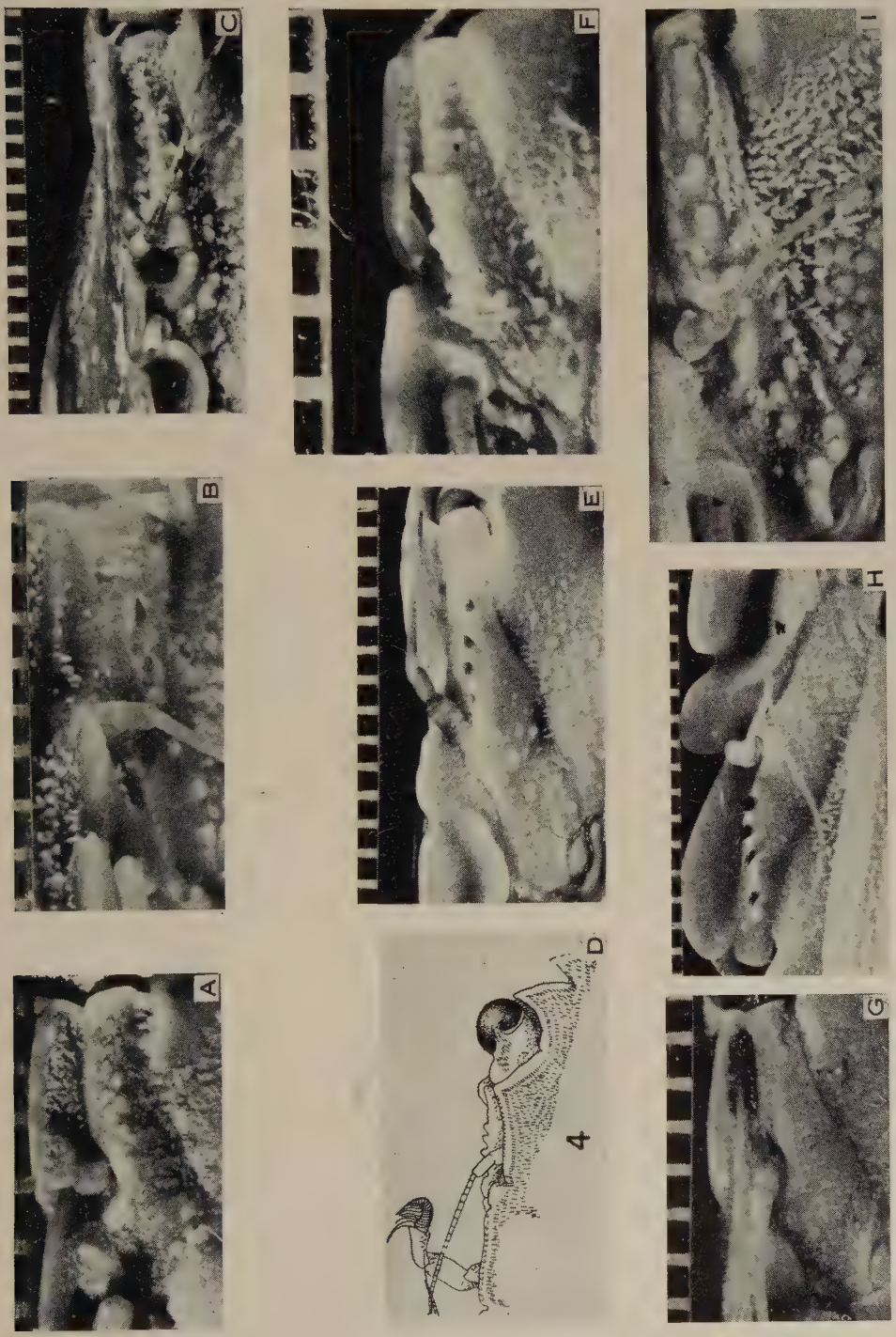
Male abdomens. *A*, *T. admete*; *B*, *T. annulipes*; *C*, *T. chaptali*; *D*, *T. coeruleipes*; *E*, specimen resembling *T. coeruleipes*; *F*, *T. crenata*; *G*, *T. danae*; *H*, *T. inhacae*; *I*, *T. integra*; *J*, *T. macropus*.

AUSTRALIAN PORTUNIDS. I



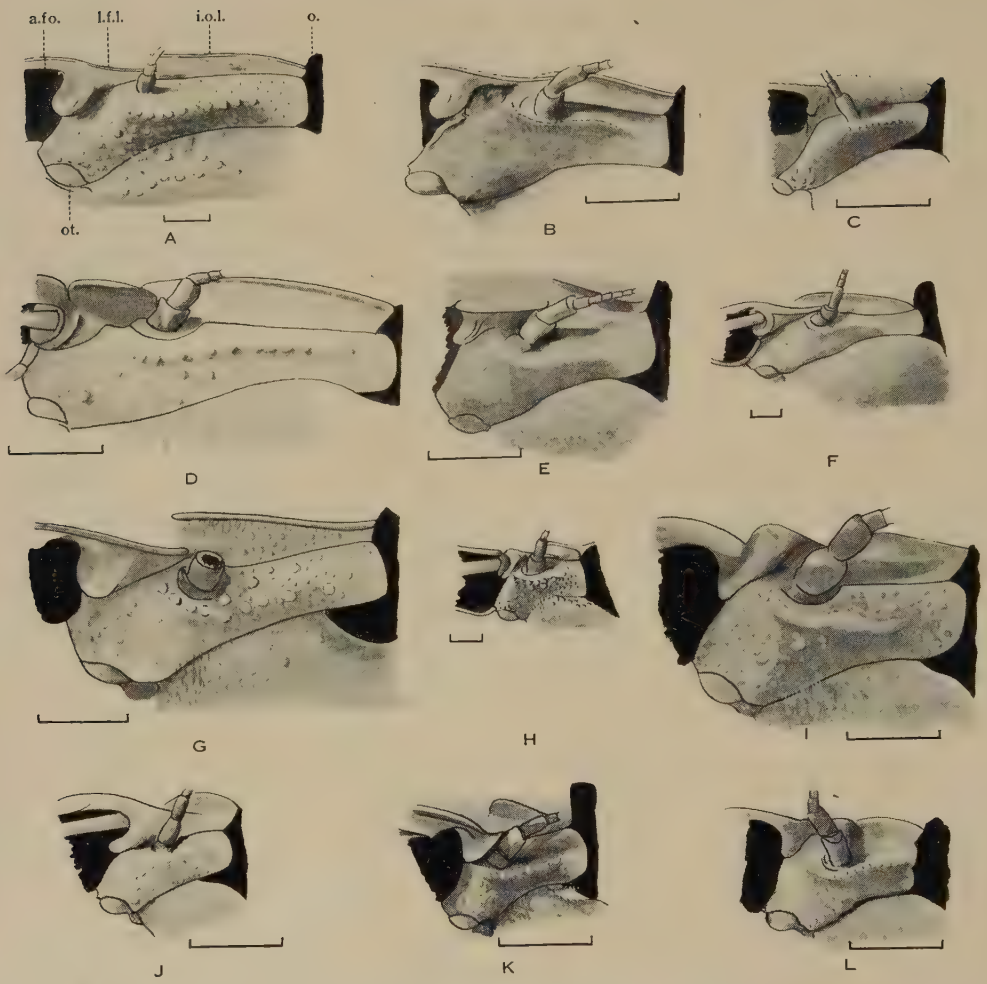
Male abdomens. *K*, *T. picta*; *L*, *T. prymna*; *M*, *T. quadrilobata*; *N*, *T. sexlobata*; *O*, *T. sima*; *P*, *T. spinimana*; *Q*, *T. squamosa*; *R*, *T. stimpsoni*; *S*, *T. trilineata*.

AUSTRALIAN PORTUNIDS. I



Basal antennal joints. *A*, *T. annulipes*; *B*, *T. coeruleipes*; *C*, *T. crenata*; *D*, *T. dakini*; *E*, *T. prymna*; *F*, *T. quadrilobata*; *G*, *T. sima*; *H*, *T. spinimana*; *I*, *T. stimpsoni*.

AUSTRALIAN PORTUNIDS. I



Basal antennal joints (wash drawings of specimens too small for satisfactory photographs). Scale lines, 1 mm. *A*, *T. admete*; *B*, *T. chaptali*; *C*, *T. cooperi*; *D*, *T. danae*; *E*, *T. inhacae*; *F*, *T. integra*; *G*, *T. intermedia*; *H*, *T. macropus*; *I*, *T. picta*; *J*, *T. squamosa*; *K*, *T. sexlobata*; *L*, *trilineata*. *a.fo.*, Fossa of first antenna; *i.o.l.*, inner orbital lobe; *l.f.l.*, lateral frontal lobe; *o.*, orbit; *ot.*, otolith.

THE IDENTIFICATION AND NOMENCLATURE OF THE SURFACE WATER MASSES IN THE TASMAN SEA (DATA TO THE END OF 1954)

By D. J. Rochford*

[*Manuscript received May* 27, 1957]

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Summary

In this paper an examination of all available data on the hydrological characteristics of the Tasman Sea, prior to and including the year 1954, has permitted the identification and naming of eight surface water masses. Certain of their properties and general features of their season and region of occurrence and method of formation are summarized.

Although little quantitative data are available some general features of the circulation of these water masses in the Tasman Sea are deduced from a study of their seasonal occurrence in relation to source regions.

The Coral Sea water mass (chlorinity 19·60–19·70‰, temperature 20–26°C) flows from a source region in the north-west Coral Sea along the western side of the Tasman Sea and reaches maximum velocity off Sydney in October–December. The South Equatorial (chlorinity 19·50–19·60‰, temperature 24–26°C) also flows

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south along the western side of the Tasman Sea but reaches maximum velocity between February and March. These two water masses constitute the East Australian current.

The Sub-Antarctic (chlorinity 19·15–19·30‰, temperature 10–14°C) is found at the surface in the south-eastern Tasman Sea between July and September. The Central Tasman (chlorinity 19·65–19·75‰, temperature 15–20°C) flows to the west from its region of formation and generally flows north along the southern New South Wales coast in late winter. The South-west Tasman (chlorinity 19·50–19·60‰, temperature 12–15°C) flows to the east in latitude 38° S. and curves south in a clockwise gyral off eastern Tasmania between October and December. The North Bass Strait (chlorinity 19·65–19·75‰, temperature 12–17°C) flows from South Australia to the eastern approaches of Bass Strait. The East Central New Zealand (chlorinity 19·10–19·30‰, temperature 15–20°C) flows west through Cook Strait into the Tasman Sea in midsummer. The East and West Tasmanian (chlorinity 19·40–19·50‰, temperature 10–14°C) form in midwinter in the southern part of Bass Strait and flow along the east and west coasts in the spring.

I. Introduction

In 1874 H.M.S. *Challenger* visited Australian waters in the course of her famous world-wide oceanographical cruise and occupied a number of stations in the Tasman and Coral Seas. Wüst (1929) has transformed her density data for the preparation of a longitudinal salinity section of the western Pacific. Use has been made of these data, despite possible long-term secular effects. The salinity-temperature data from a station of S.M.S. *Planet* in the northern Coral Sea in 1913 have also been used despite similar objections.

Halligan (1907) investigated the sand drift problem on the New South Wales coast and subsequently extended his studies to the ocean currents of Australia (1921). In 1930 he stated: "We are still not entitled to speak, except in very general terms of this [i.e. the East Australian current], or indeed of any of the currents within the Australian region, an undesirable state of affairs which it is hoped will be remedied in the early future." Unfortunately, his hopes of such oceanographical investigations were not realized, even in part, until much later.

Commencing in 1938, this Division carried out a series of combined oceanographical and fishing cruises along the east Australian coast with its F.R.V. *Warreen*. However, the fishery demands permitted little systematic oceanographical sampling; and in any case because of the limited size and capabilities of the vessel the offshore investigations could not be extended much beyond slope waters. On a cruise in August 1940 sections were worked at approximately 1 degree of latitude apart, to a distance of some 60–80 nautical miles offshore along the east Australian coast between latitudes 28° and 44° S. Subsequent to this, a similar cruise in January 1941 and part of a cruise in January 1942 were completed before wartime conditions prevented further sampling.

The data collected by F.R.V. *Warreen* were almost entirely within the shelf and slope regions but, because of the major influence of oceanic circulation on the properties of eastern Australian shelf and slope waters, some evidence regarding the oceanic water masses and their seasonal cycles in the Tasman Sea proper can be gained from them.

In 1950, R.R.S. *Discovery II* sampled waters off the east Australian coast, and occupied a line of stations across the Tasman Sea between Sydney and New Zealand. Also the Danish frigate *Galathea* visited Australian waters in 1951 but only a small number of oceanographical stations was occupied in the Tasman Sea area.

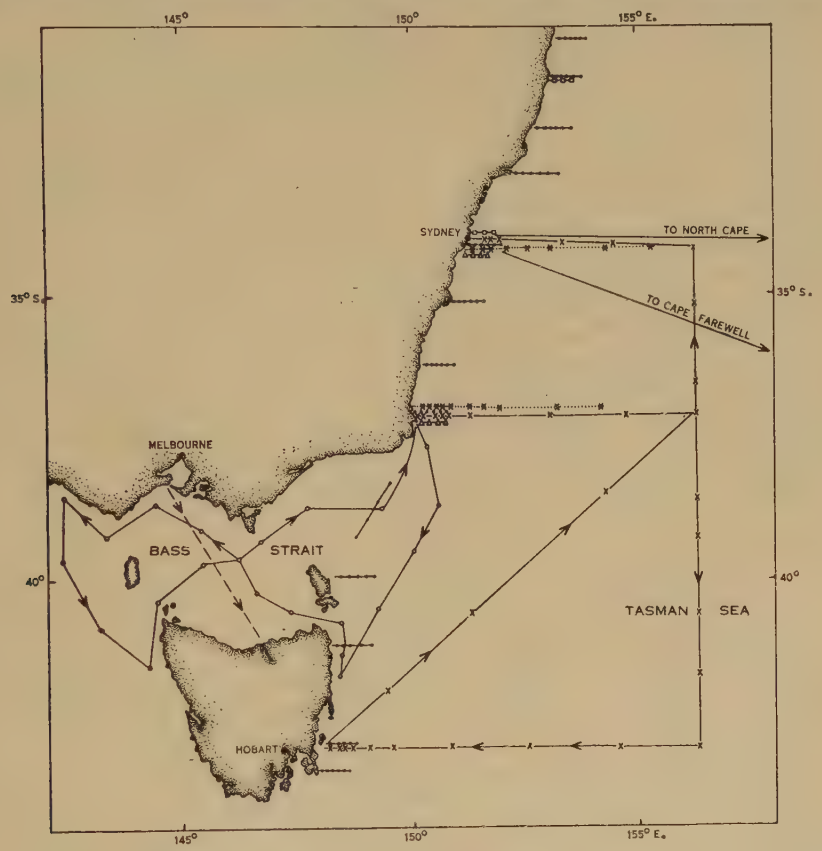

Fig. 1.—The routes in the south-west Tasman Sea of the various ships whose data are used in this paper.

●——● *Warreen.*
—— *Discovery II.*
×——× *Derwent Hunter,* south-west Tasman.
○——○ *Derwent Hunter,* Bass Strait.
□——□ *Warrego.*
△——△ *Barcoo.*
——— *Wanganella.*
– – – – *Taroona.*

The successful use by Veen (1951) of surface collections from commercial ships in the Java Sea prompted in 1952 an approach to the Huddart Parker Company of Sydney for cooperation in the collection of surface samples from T.S.M.V. *Wanganella* during her regular voyages between Sydney and Wellington and between Sydney and Auckland. This cooperation was readily extended, and the collection of

surface temperature data and water samples from the *Wanganella* commenced in December 1952. In 1953 H.M.A.S. *Barcoo* and *Warrego* sampled New South Wales coastal and slope waters in the course of hydrographic operations. In mid 1954 permission was given by the Huddart Parker Company for T.S.S. *Taroona* to collect surface samples across Bass Strait, and these chlorinity and temperature data have also been used.

In 1954 the F.R.V. *Derwent Hunter* was used for a more detailed examination of a south-western sector to the west of longitude 156° E., between latitudes 34° and 43° S. Two cruises in 1954 were completed, one in February and the other in December. Water sampling to 1000 m was carried out on each of these cruises. Some use has been made of the physical data from cruises in Bass Strait and its approaches in April and November 1954.

The geographical distribution of the stations occupied in the Tasman Sea and Bass Strait between 1938 and 1954 is shown in Figure 1. Of a total of 5238 stations occupied by vessels of this Division in the Tasman Sea and Bass Strait between 1938 and 1954, only 12 per cent. were full vertical stations to depths of 500–1000 m. Prior to 1950 no station beyond 60 miles off the coast had been worked. Even in 1954 only 68 stations were occupied east of this limit. The greater part of the data available for the Tasman Sea up to the end of 1954, therefore, is compiled from surface stations only. The limitations of these surface data are discussed in Section V(*b*).

II. Material and Methods

The methods followed in the collection and analysis of sea-water samples have been given previously (C.S.I.R.O. Aust. 1951*a*).

Since 1954, however, the majority of chlorinity determinations have been made with a chlorinity-temperature meter (Hamon 1956) with an accuracy of ±0·02‰.

Because no facilities for phosphate analyses were available on board F.R.V. *Derwent Hunter* total phosphorus values alone have been used in this paper. These have been determined by the perchloric acid method of Hansen and Robinson (1953). Phosphate and nitrate values have been expressed as micrograms of phosphate phosphorus and nitrate nitrogen per litre respectively, without salt correction.

Samples from merchant ships were taken at a depth of about 5 m. Water temperatures on the *Wanganella* prior to April 1954 were, and on the *Taroona* are still, taken by the ship's engine room thermometers. These have been checked against standard thermometers and found accurate to ±0·5°F.

In April 1954 a Negretti and Zambra thermograph, model M/2238B, with a 6 in. drum, was installed on the *Wanganella*, and surface temperatures are now read from it with a probable accuracy of ±0·25°C, which is of the same order as before. This relatively low order of accuracy must be borne in mind when using these surface temperatures.

Sources of Data.—The data from the following vessels have been published:

F.R.V. *Warreen* (C.S.I.R.O. Aust. 1951*a*, 1951*b*),

F.R.V. *Derwent Hunter* (C.S.I.R.O. Aust. 1956*a*),

T.S.M.V. *Wanganella* (C.S.I.R.O. Aust. 1955, 1956*b*),
T.S.S. *Taroona* (C.S.I.R.O. Aust. 1956*a*),
H.M.A.S. *Warrego* (C.S.I.R.O. Aust. 1954),
H.M.A.S. *Barcoo* (C.S.I.R.O. Aust. 1954),
R.R.S. *Discovery II* ("Discovery II" 1941; C.S.I.R.O. Aust. 1953),
R.R.S. *Dana* (Carlsberg Foundation, Copenhagen 1937),
H.M.S. *Challenger* (Buchanan 1884),
S.M.S. *Planet* (R. (Reichard) 1911).

Fig. 2.—Bathymetric chart of the Tasman and Coral Seas, with contours at 1000, 2000, and 5000 m only. Insert chart shows the bathymetry of Bass Strait, at contour intervals of 30 fm (55 m), 40 fm (73 m), and 45 fm (82 m). The stations on the dotted line are those used in Section IV, with symbols as in Fig. 3.

Limits of the Tasman and Coral Seas.—Figure 2, which is adapted from Sheet "A III" of the "Carte Générale Bathymétrique des Océans", shows the principal bathymetric features of the Tasman and Coral Seas and the arbitrary boundaries used in this investigation.

III. Identifying Properties of Water Masses

Various conservative physical and chemical properties were used to identify the principal water masses which, by their mixing interactions during movement from their source regions, determine the major physical and chemical characteristics of the Tasman Sea. The mixed bodies of water thus formed in coastal regions are subject particularly to local external effects of heating, cooling, evaporation, and fluvial dilution; these factors greatly complicate the interpretation of the data in terms of simple water-mass mixing, especially as these local external effects vary considerably with the seasons.

Instead of the salinity-temperature relationship (Helland-Hansen 1916), the chlorinity-temperature relationship has been used to identify water masses because it is not certain that salinity derived from chlorinity by the Knudsen equation is correct for some regions of the Tasman Sea, especially in eastern Australian and New Zealand coastal waters.

Following the suggestion by Harvey (1948), total phosphorus whenever available has also been used as a supplementary identifying property.

The term *primary water mass* is used to denote an extensive body of water formed by the operation of certain factors in its source region and possessing properties which, though they vary from year to year, are still within a sufficiently restricted range for separate identification even at some distance from the source region. The various mixtures between the primary water masses give rise to less extensive secondary ones which are termed *derived water masses*. Local external factors can sometimes consistently alter the properties of these derived water masses and form a third type of very restricted distribution, termed a *modified water mass*.

The following illustrates such a relationship between four of the Tasman Sea water masses:

Primary Water Mass	Derived Water Mass	Modified Water Mass
Central Tasman + Sub-Antarctic	South-west Tasman (fluvial dilution)	East Tasmanian

Water masses can also be denoted as *internal water masses*—those which are formed within an area, and *external water masses*—those which originate outside and subsequently move into an area. Comprehensive data are usually collected in certain seasons and regions only, rather than simultaneously over the whole area being studied. These regional and seasonal data are analysed for water-mass structure and conclusions from them fitted into a general picture of the area as a whole. The water masses from such regional data are termed *regional*. These are eventually fused into one of the three more general types already considered.

IV. The Chlorinity-Temperature Relationships along a Meridional Section of the Coral and Tasman Seas

In this paper a *surface water mass* is considered to be the body of water extending from the surface either down to the lower limit of the homogeneous chlorinity layer (as at station 188/54, Fig. 3*A*), or to the depth at which an intermediate layer of uniform chlorinity first appears (station 3665, Fig. 3*A*). Using data from the stations on the dotted lines of Figure 2, a composite meridional section of the vertical chlorinity-temperature relationship was made (Fig. 3*A*). Despite the period of years

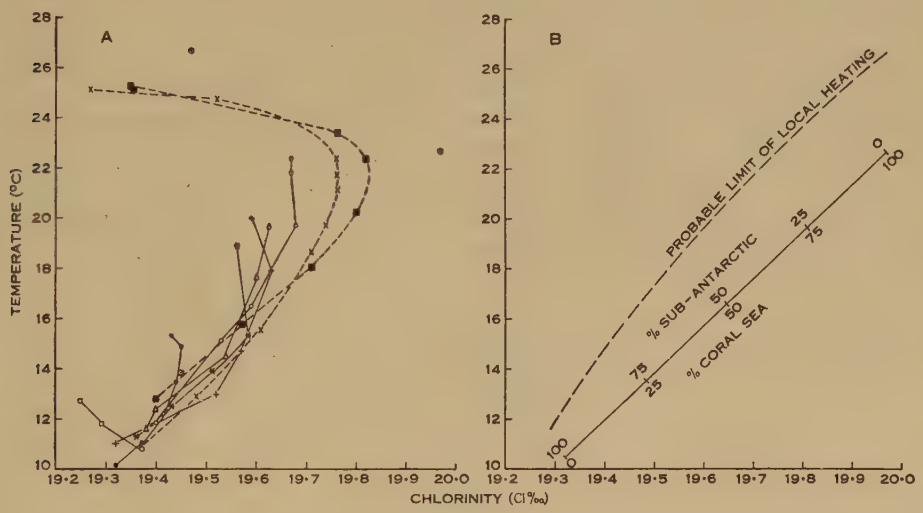

Fig. 3.—*A*, north-south variation in chlorinity-temperature relationships of Tasman Sea waters along a composite section extending from lat. 15 to 45° S. (dotted lines in Fig. 4). The stations listed below are arranged in order of increasing latitude south.

□- - - -□ *Planet*, June 1908: st. 13. ⊙ *Challenger*, August 1874: st. 180. ×- - - -× *Dana*, February 1929, st. 3665. *Derwent Hunter*, November–December 1954: ○———○ st. 188/54, +———+ 187/54, △———△ 186/54, *———* 185/54, ●———● 169/54, □———□ 172/54.

B, mixing diagram for estimating percentages of Coral Sea and sub-Antarctic water masses in Tasman Sea surface waters.

between the sampling of stations on the northern and southern parts of this section, it is proposed to regard it as representative of chlorinity-temperature conditions in the spring and summer of each year. Accepting these limitations it can be seen that for stations south of station 188/54 in latitude 34° S., each chlorinity-temperature curve consists of a surface layer of variable depth in which the chlorinity remains constant but the temperature decreases. For the remainder of the curve the temperature and chlorinity both vary uniformly with depth.

In the Coral Sea region this layer of constant chlorinity is overlain by a surface layer of relatively constant temperature, but with chlorinity rapidly increasing with depth. In the deeper parts of the chlorinity-temperature curves it can also be seen that the Coral Sea waters below 500 m differ from the deep Tasman Sea waters.

It is possible that this difference is largely caused by higher temperatures relative to chlorinity in the deeper layers of the Coral Sea. Transfer of heat from the surface to deeper levels without appreciable change in chlorinity could bring this about. Even small annual increases in the temperature of these deeper layers could be cumulative because of the relative isolation of the Coral Sea basin (Fig. 2).

The following interpretation is offered of the general shape of the chlorinity-temperature curves in these two seas. At varying depths between 500 and 1000 m, there exists a Sub-Antarctic water mass with properties approaching those of the surface Sub-Antarctic waters encountered off eastern Tasmania (Table 1). Deacon (1937) has suggested a chlorinity of 19·32‰ and a temperature of 10·5°C as the upper limit of these properties in the deep Sub-Antarctic water mass. In the Coral Sea region a source exists of a water mass of very high chlorinity (>19·90‰) and moderate temperature (22–24°C), an indication of which was found at 100 fm on *Challenger* station 180. This Coral Sea water mass flows southward, overriding a probable slow northward movement of the Sub-Antarctic water mass. Progressive mixing between these two water masses produces at subsurface levels water with properties intermediate between those of the two primary sources.

TABLE 1

REGIONAL SURFACE WATER MASSES OF SOUTH-WEST TASMAN TO THE EAST AND NORTH-EAST OF TASMANIA, FEBRUARY 1954

Location of Water Mass	Chlorinity (‰)	Temperature (°C)
37° 04′ S., 156° 01′ E.	19·70	21·20
Intermediate depths, eastern Tasmanian offshore waters (42° 06′ S., 148° 39′ E.)	19·62	13·50
42° 33′ S., 156° 15′ E.	19·28	14·60

In the Coral Sea there also exists at the surface a water mass with chlorinity below 19·40‰ and temperatures greater than 25°C. This water mass was found at *Dana* station 3665, at *Planet* station 13, and to a lesser extent at *Challenger* station 180. Subsequently this was termed the South Equatorial water mass (Section VII); it flows in February, according to Schott (1935), between Norfolk I. and New Caledonia into the Coral and Tasman Seas. The surface zone of uniform chlorinity but varying temperature, particularly evident at station 188/54, could be an effect of local heating on a mixture of Coral Sea and Sub-Antarctic waters but could also be caused by the southern movement, at the surface, of the South Equatorial water mass.

In the Coral Sea in June 1908 and February 1929, a surface South Equatorial water mass of some 100 m depth overlay an intermediate stratum of the Coral Sea water mass of about the same thickness. In the Tasman Sea proper the depth of the uniform-chlorinity layer varied from about 100 to less than 50 m in the extreme south-west.

Figure 3*B* shows the chlorinity-temperature properties that mixed waters of different percentages of Coral Sea and Sub-Antarctic waters would have during the season of minimum temperatures, and the probable upper limit of seasonal temperature increase. For the Coral Sea Schott's (1935) data, for the Sub-Antarctic Deacon's (1937) data, and for the south-west Tasman the data from the 1954 investigations by F.R.V. *Derwent Hunter* (Fig. 1) have been used to estimate the annual temperature range.

V. The Seasonal Reappearance during the Period 1940 to 1954 of the Water Masses of the Tasman Sea

From a consideration of the latitudinal change in the shape of the temperature-chlorinity relationship curves (Section IV), it was suggested that three water masses were primarily responsible for surface conditions in the Tasman and Coral Seas during spring and summer. These water masses were identified as the South Equatorial (moderate chlorinity, highest temperature), the Coral Sea (highest chlorinity, moderate temperature), and the Sub-Antarctic (lowest chlorinity and temperature). The South Equatorial and the Coral Sea water masses flowed south at the surface whilst the Sub-Antarctic, for the greater part, flowed north at an intermediate level.

In this section of the paper an examination of all available chlorinity-temperature data between 1940 and 1954 shows that these three water masses are always of major importance in the seasonal pattern of the Tasman Sea, and that the derived water masses of this region are formed by mixing between them.

The complete range of water masses which are considered of permanent significance in the surface zone of the Tasman Sea are listed in Table 2, with their annual ranges in temperature and chlorinity, mean total phosphorus, probable source region, and method of formation. Because much of this information is based upon surface samples in the region between Sydney and New Zealand, some correction of these properties may be necessary as more extensive data are collected, but the continued appearance of these water masses during 1940 to 1954 is considered proof of their separate identity.

(*a*) *The Primary, Locally Derived, and Modified Regional Surface Water Masses of Eastern Australian Coastal and Shelf Waters from F.R.V.* Warreen *Data*

(i) *August* 1940.—Figure 4*A* shows a typical family of curves for the *Warreen* stations along a section in latitude 32° 42′ S. From these curves the properties of the least number of regional surface water masses from which the others could be formed by mixing were listed. By comparing the regional water masses of each *Warreen* section and allowing for latitudinal heat losses and slight changes in chlorinity, those water masses with similar properties were eliminated, thus reducing the total for the whole area to the minimum number from which the original list could have been formed by mixing and local heating or cooling. The major water masses of each section for August 1940 are listed in Table 3*A*. Because sampling was not carried out below 600 m on these cruises the deep-water mass had to be arbitrarily chosen at a chlorinity of 19·40‰. Table 3*A* gives not only the median temperature but also its range of variation, and demonstrates the uniformity of

TABLE 2

PROPERTIES AND CHARACTERISTICS OF SURFACE TASMAN SEA WATER MASSES

Water Mass	Annual Range in Tasman Sea		Mean Total P (μg/l.)	Source Region	Status	Probable Method of Formation	Season of Maximum Occurrence	Region of Occurrence in Tasman Sea
	Chlorinity (‰)	Temp. (°C)						
Coral Sea	19·60–19·70	20–26	11 {Oct., 11 Dec., 10	NW. Coral Sea	Primary external	Isolation and local evaporation of equatorial waters	Oct.–May	Western Tasman Sea
South Equatorial	19·50–19·60	24–26	10*	South Equatorial current	Primary external	Dilution by precipitation of subtropical waters	Feb.–May.	Western Tasman Sea
Sub-Antarctic	19·15–19·30	10–14	25 {Feb., 20 Dec., 30	Southern Ocean	Primary external	Mixing between subtropical and Antarctic waters	May–Sept.	Surface S. of lat. 43° S., intermediate depths throughout
Central Tasman	19·65–19·75	15–20	16 {Oct., 19 Dec., 12	Central Tasman (tropical convergence)	Primary internal	Cooling at intermediate depths of Coral Sea waters	June–Dec.	South Tasman Sea
South-west Tasman	19·50–19·60	12–15	19 {Oct., 23 Dec., 15	Eastern approaches to Bass Strait	Derived	Mixing between Central Tasman and Sub-Antarctic waters	June–Dec.	SW. Tasman Sea S. of latitude 38° S.
North Bass Strait	19·65–19·75	12–17	10 {Mar., 10 Nov., 10	South Australian gulfs	Derived	Evaporation of Bight waters in South Australian gulfs	Oct.–Apr.	North Bass Strait from western to eastern approaches
East Central New Zealand	19·10–19·30	15–20	20*	East of Cook Strait	Derived	Heating of Sub-Antarctic waters	Dec.–Apr.	West of North Island, New Zealand
E. Tasmanian–W. Tasmanian	19·40–19·50	10–14	16 {Mar., 15 Nov., 17	North coast of Tasmania	Modified	Fluvial dilution of Bass Strait waters	Apr.–Dec.	Coastal region of Tasmania

*One voyage only (Dec.).

chlorinity-temperature properties at that depth. By plotting the chlorinity-temperature relationships of these sectional water masses (Fig. 4*B*), the regional water masses given in Table 3*B* were deduced.

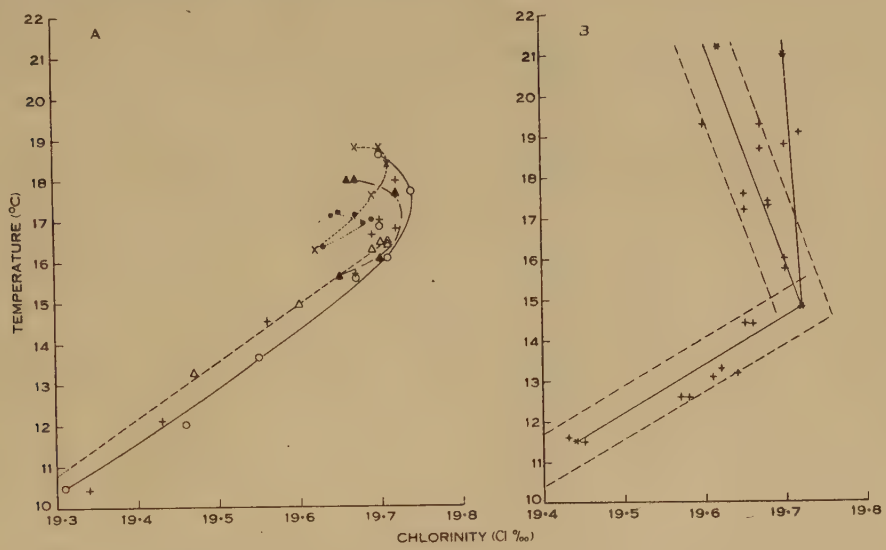

Fig. 4.—*A*, chlorinity-temperature relationships of the coastal and shelf waters in lat. 32° 42′ S., August 1940.

● 64/40. ▲ 66/40. + 68/40.
× 65/40. ○ 67/40. △ 69/40.

B, relationships of the primary surface water masses (*) and locally derived and modified surface water masses (+) of the east Australian coast and shelf waters, August 1940.

(ii) *January* 1941.—A similar procedure as for August 1940 was followed for shelf and slope waters sampled during January 1941. In this month the vertical and horizontal spread of chlorinity-temperature properties was much greater than in August 1940. Figure 5*B* illustrates the range of chlorinity-temperature characteristics along a section extending 30–40 miles off Maria I. in latitude 42° 42′ S. Various combinations of the East Tasmanian, the Coral Sea, the offshore intermediate, and the deep Sub-Antarctic water masses are revealed. The offshore intermediate water mass had chlorinity-temperature properties which were very similar to the late spring properties of the South-west Tasman water mass (Table 4).

Off the New South Wales coast in latitude 33° 59′ S. (Table 5*A*) the regional offshore intermediate water mass had chlorinity, and to a lesser extent temperature, properties similar to those of the Central Tasman water mass occurring at the surface of the central Tasman Sea in June 1954 (Fig. 6*C*).

Without fuller knowledge of the circulation and other identifying properties it would be premature to claim that the Central Tasman is the same as the regional offshore intermediate water mass. Schott (1935) plotted a tropical convergence south of Lord Howe I. and extending north-east to the Kermadec group in August–September (Plate XXX) but only to Norfolk I. in February–March (Plate XXIX). The sinking of Coral Sea water along this convergence in November–December could

TABLE 3

A. SECTIONAL ANALYSIS OF WATER MASSES, AUGUST 1940

Latitude (S.)	Onshore Water Mass		Offshore Water Mass		Offshore Intermediate Water Mass		Offshore Deep Water Mass	
	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)
30° 18′	19·60	19·30	19·62	21·20	—	—	19·40	11·80 ± 0·02
30° 55′	19·67	18·70	19·67	19·30	—	—	19·40	11·85 ± 0·15
31° 45′	19·65	17·60	19·70	21·00	—	—	19·40	11·60 ± 0·50
32° 42′	19·65	17·20	19·70	18·80	19·73	17·70	19·40	11·80 ± 0·30
34° 04′	19·68	17·30	19·72	19·10	—	—	19·40	11·50 ± 0·15
35° 07′	19·66	14·40	19·68	17·40	—	—	19·40	11·85 ± 0·15
36° 16′	19·65	14·40	19·70	15·80	—	—	19·40	11·80 ± 0·25
37° 02′	19·64	13·20	19·70	16·00	—	—	19·40	11·40 ± 0·05
39° 57′	19·58	12·60	19·62	13·30	—	—	—	—
42° 37′	19·45	11·50	19·61	13·10	—	—	19·40	11·25 ± 0·25
43° 10′	19·43	11·60	19·57	12·60	—	—	19·40	11·10 ± 0·40

B. PROPERTIES OF REGIONAL SURFACE WATER MASSES IN COASTAL AND SHELF REGIONS, AUGUST 1940

Water Mass	Latitude of Occurrence (S.)	Chlorinity (‰)	Temperature (°C)
Southern Queensland offshore water mass	30° 18′	19·62	21·20
Northern N.S.W. offshore surface water mass	31° 45′	19·70	21·00
Southern N.S.W. offshore surface water mass	36° 16′ 37° 02′	19·70 19·70	15·80 16·00
		Mean: 19·70	15·90
		19·72*	14·80*
East Tasmanian onshore surface water mass	42° 37′ 43° 10′	19·45 19·43	11·50 11·60
		Mean: 19·44	11·55

*Value obtained by extrapolation (Fig. 4*B*).

form this intermediate water mass, part of which, spreading from the convergence region in a southerly and westerly direction, would have to lose heat without appreciable change in chlorinity and subsequently rise to the surface as the Central Tasman

TABLE 4

REGIONAL SURFACE WATER MASSES OF SOUTH-WEST TASMAN, DECEMBER 1954

Water Mass	Chlorinity (‰)	Temperature (°C)	Total P (μg/l.)
Coral Sea	19·65	23·00	10
South-west Tasman	19·51	12·50	15
Sub-Antarctic	19·27	12·50	30

water mass of early winter. To maintain a high chlorinity level, vertical mixing with deep Sub-Antarctic water would have to be minimal. Whilst conditions for the

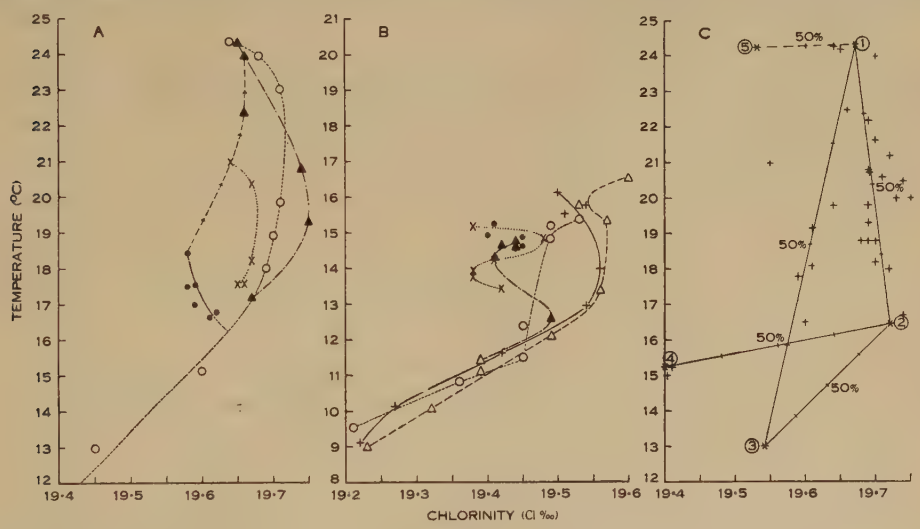

Fig. 5.—*A*, chlorinity-temperature relationships of the coastal and shelf waters in lat. 31° 51′ S., January 1941.

● 23/41. ▲ 25/41.
× 24/41. ○ 26/41.

B, chlorinity-temperature relationships of the coastal and shelf waters in latitude 42° 42′ S., January 1941.

● 57/41. ▲ 59/41. + 61/41.
× 58/41. ○ 60/41. △ 62/41.

C, relationships of the primary (*) and locally derived and modified surface water masses (+) of the east Australian shelf and slope waters, January 1941.

Numbers denote water masses listed in Table 5*B*; connecting which scales of percentage mixing have been drawn.

formation of the Central Tasman water mass from a converging Coral Sea water mass could exist in the south Tasman Sea, further evidence will have to be sought and critically examined before such a mode of formation can be determined.

Figure 5*A* illustrates a common occurrence in New South Wales coastal waters during the summer period. The coastal station 23/41 had bottom waters whose chlorinity-temperature properties were practically identical with those at a depth of 230 m in the slope waters at station 26/41. Nutrient values (C.S.I.R.O. Aust. 1951*b*) leave no doubt that these deep slope waters were the source of this bottom shelf coastal water. The surface coastal waters were several degrees warmer than the bottom waters but were also greatly influenced by deep slope water. At greater distances offshore the influence of the surface offshore water mass became progressively greater, but slope waters of about the same properties were encountered at all stations. It seems likely that deep slope waters moved into the bottom coastal region and circulated seaward at the surface.

From the chlorinity-temperature curves at each section, the sectional water masses along the east Australian coast in January 1941 have been determined and are listed in Table 5*A*. By selecting those water masses in Table 5*A* which are clearly homologous, and determining their mean properties, the regional water masses listed in Table 5*B* have been identified.

The relationship between these primary water masses and the regional water masses of each section are shown in Figure 5*C*. Except for a small group which lies outside the various mixing paths and was probably formed by fluvial dilution, most of these sectional water masses were formed by horizontal or vertical mixing between the primary water masses of Table 5*B*.

TABLE 5

A. SECTIONAL ANALYSIS OF WATER MASSES, JANUARY 1941

Latitude (S.)	Onshore Surface Water Mass		Offshore Surface Water Mass		Offshore Intermediate Water Mass		Offshore Deep Water Mass	
	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)
28° 41′	19·66	22·50	19·65	24·50	19·70	18·80	19·40	11·90±0·30
30° 18′	19·69	19·30	19·70	24·00	19·73	20·00	19·40	11·60±0·05
30° 56′	19·69	19·80	19·67	24·30	19·71	20·50	19·40	11·50±0·30
31° 51′	19·59	17·80	19·65	24·20	19·75	20·00	19·40	11·60*
32° 42′	19·61	18·10	19·64	24·30	19·74	20·50	19·40	11·70±0·10
33° 59′	19·69	20·80	19·69	20·80	19·74	16·50	19·40	11·50±0·25
35° 13′	19·55	21·00	19·69	22·20	19·72	18·00	19·40	11·60±0·30
36° 13′	19·61	19·15	19·70	21·65	—	—	19·40	11·30±0·05
37° 06′	19·64	19·80	19·72	21·20	—	—	19·40	11·60±0·15
39° 57′	19·68	18·80	19·69	18·80	—	—	19·40	11·30±0·20
41° 20′	19·41	15·30	19·70	18·20	—	—	19·40	11·30±0·15
42° 42′	19·40	15·00	19·60	16·50	19·55	13·00	19·40	11·30±0·20

*One station only.

TABLE 5 (*Continued*)

B. REGIONAL SURFACE WATER MASSES IN COASTAL AND SHELF REGIONS, JANUARY 1941

Water Mass	Latitude of Occurrence (S.)	Chlorinity (‰)	Temperature (°C)
Northern N.S.W. offshore surface water	28° 41′	19·65	24·50
	30° 18′	19·70	24·00
	30° 56′	19·67	24·30
	31° 51′	19·65	24·20
	32° 42′	19·64	24·30
		Mean: 19·66	24·30
Central N.S.W. offshore intermediate water (subsurface chlorinity max.)	33° 59′	19·74	16·50
East Tasmanian coastal water	41° 20′	19·41	15·30
	42° 42′	19·38	15·20
		Mean: 19·40	15·30
East Tasmanian offshore intermediate water	42° 42′	19·54	13·00
Central N.S.W. offshore water mass	33°	19·53	24·50

In Section VI it is suggested that the South-west Tasman water mass is formed by mixing between a Central Tasman water mass, with properties similar to the summer offshore intermediate water mass of New South Wales, and the deep Sub-Antarctic water mass. It is possible therefore that the surface South-west Tasman water mass east of Tasmania in November 1954 and the offshore intermediate water mass in the same region in January 1941 were the same. This implies a convergence zone where the South-west Tasman water mass, formed in late spring, can sink and form an intermediate stratum in the following summer (see Section V(*c*)(v)).

(iii) *January* 1942.—In January 1942 stations were occupied only between latitudes 28° and 34° S., and the sectional water masses observed are listed in Table 6*A*.

By comparing Figures 7*A* and 5*A* it can be seen that the surface chlorinities were much higher in January 1942 than in January 1941, although temperatures were comparable. Moreover there was no evidence of an intermediate maximum-chlorinity layer in January 1942 as there was at intermediate levels at station 25/41 in January 1941. An examination of the relationships of the dominant water masses at each latitude (Fig. 7*B*) shows that the surface, coastal, and slope water masses in January 1942 were formed by mixing between a water mass with the chlorinity-temperature

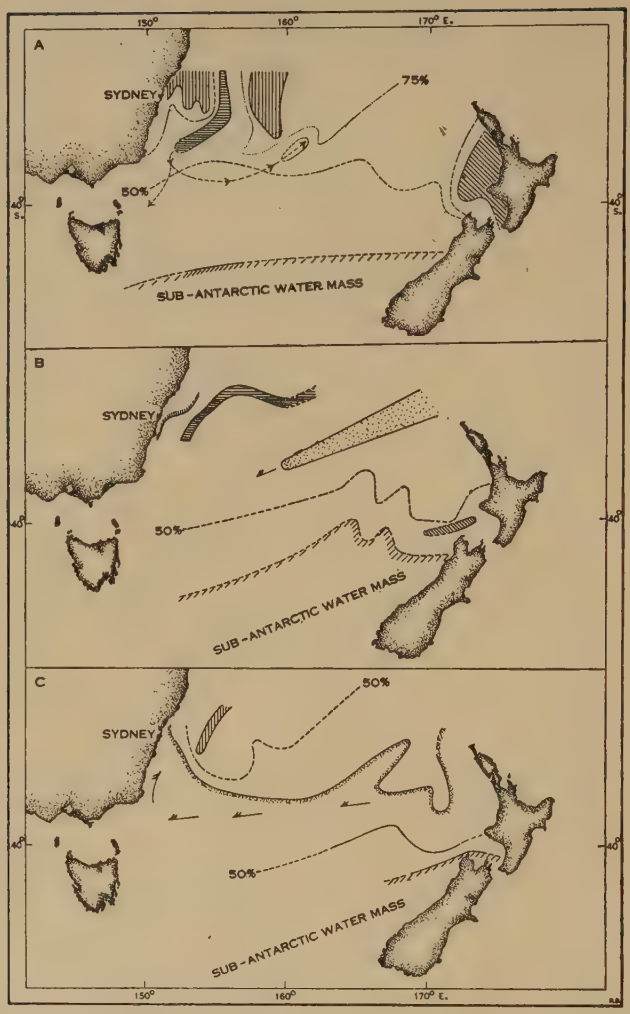

Fig. 6.—*A–C*.—Distribution of the primary water masses in the Sydney–Cape Farewell–North Cape triangle of the Tasman Sea. Barbed arrows denote paths of movement, broken lines various percentage mixtures of the primary water masses.

Water Mass	*A*. Feb. 1954		*B*. Apr. 1954		*C*. June 1954	
	Cl (‰)	Temp.(°C)	Cl (‰)	Temp.(°C)	Cl (‰)	Temp.(°C)
South Equatorial	19·54	24·10	19·52	25·20	—	—
Coral Sea	19·70	23·50	19·67	26·00	19·60	22·60
East Central New Zealand	19·30	18·90	19·17	15·00	—	—
Central Tasman	—	—	19·70	20·50	19·70	17·10
South-west Tasman	—	—	—	—	—	—
Sub-Antarctic	19·27	12·50	19·29	11·38	19·16	12·50

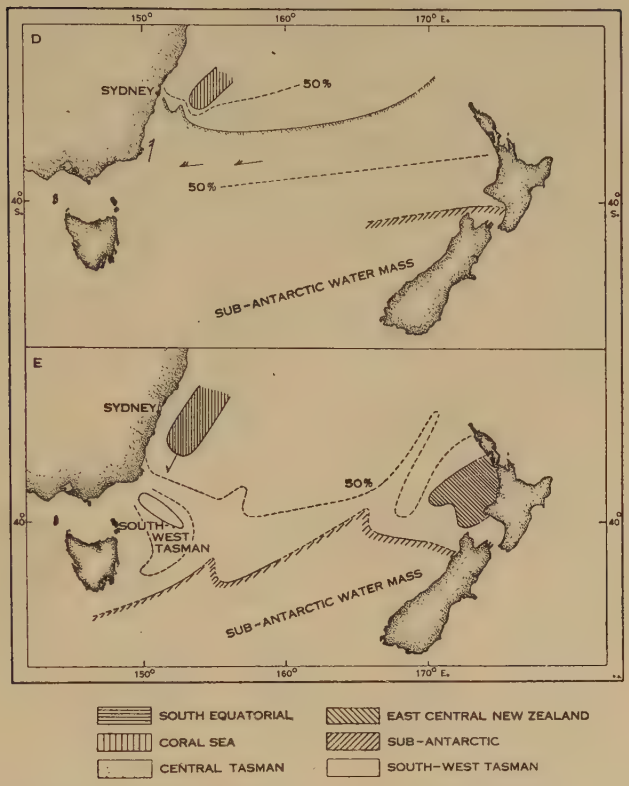

Fig. 6.—*D*, *E*.—Distribution of the primary water masses in the Sydney–Cape Farewell–North Cape triangle of the Tasman Sea. Barbed arrows denote paths of movement, broken lines various percentage mixtures of the primary water masses.

Water Mass	*D*. Sept. 1954		*E*. Dec. 1954*	
	Cl (‰)	Temp. (°C)	Cl (‰)	Temp. (°C)
South Equatorial	—	—	—	—
Coral Sea	19·53–68	20·00	19·70	22·30–60
East Central New Zealand	—	—	19·27	17·20
Central Tasman	19·65	15·40	19·68	17·70
South-west Tasman	—	—	19·50	12·50
Sub-Antarctic	19·27	11·00	19·30	11·50

* Including *Derwent Hunter* data.

properties in Table 6*B* and a Sub-Antarctic water mass. As it is not likely that Sub-Antarctic water could occur at the surface in these latitudes in summer, this mixing must have been vertical and not horizontal. Comparison of Figures 5*C* and 7*B* shows that the low-chlorinity high-temperature water mass numbered 5 in January

1941 did not occur in January 1942 within the same area of the New South Wales coastal region.

Figure 8 summarizes the *Warreen* evidence on east Australian coastal and slope water masses for 1940 and 1941. The water masses with chlorinities greater than 19·65‰ and temperatures above 20°C are considered part of the circulation of the Coral Sea water mass. The water masses with similar temperatures but chlorinities below 19·60‰ are considered part of the circulation of the South Equatorial water mass. The chlorinity value for this water mass in August 1940

TABLE 6

A. SECTIONAL ANALYSIS OF WATER MASSES, JANUARY 1942

Latitude (S.)	Onshore Surface Water Mass		Offshore Surface Water Mass		Offshore Deep Water Mass	
	Chlorinity (‰)	Temp. (°C)	Chlorinity (‰)	Temp. (°C)	Chlorinity* (‰)	Temp.* (°C)
28° 48′	19·80	22·50	19·87	23·90	19·40	11·50
30° 17′	19·80	21·00	19·82	23·40	19·40	12·00
30° 55′	19·72	21·50	19·83	24·60	19·40	12·00
31° 51′	19·72	21·30	19·87	23·80	19·40	12·00
32° 43′	19·74	21·40	19·83	24·00	19·40	12·00
33° 16′	19·76	22·00	19·81	22·70	19·40	12·00

*Only one slope station per section.

B. MEAN PROPERTIES OF THE REGIONAL SURFACE WATER MASS IN COASTAL AND SHELF WATERS BETWEEN LATITUDES 28° 48′ AND 33° 16′ S., JANUARY 1942

Water Mass	Latitude of Occurrence (S.)	Chlorinity (‰)	Temperature (°C)
N.S.W. offshore water mass	30° 35′	19·83	24·60
	32° 43′	19·83	24·00
		Mean: 19·83	24·30

(Table 3) was above this value, and it is probable that the winter boundary of this water mass lies farther to the north than was reached on this cruise. However, in Figure 8 it has been grouped as of South Equatorial origin. The water masses with chlorinities greater than 19·70‰ but with temperatures less than 17°C have been identified as Central Tasman.

The summer intermediate water mass of eastern Tasmania (Table 5*B*) could not on the evidence of the 1940–41 data be considered of major importance. However, from later evidence (Table 4) it is clear that the South-west Tasman water mass,

with similar properties, is a persistent seasonal feature of this region. Accordingly this 1941 intermediate water mass has been identified as South-west Tasman. Coastal water masses with chlorinities less than 19·45‰ and temperatures below 16°C were found off Tasmania on both winter and summer cruises of 1940 and 1941. Later evidence (Section V(*c*)(i), (ii)) indicates that water masses with similar properties occur in other years. The 1940–41 occurrences have therefore been identified as East Tasmanian.

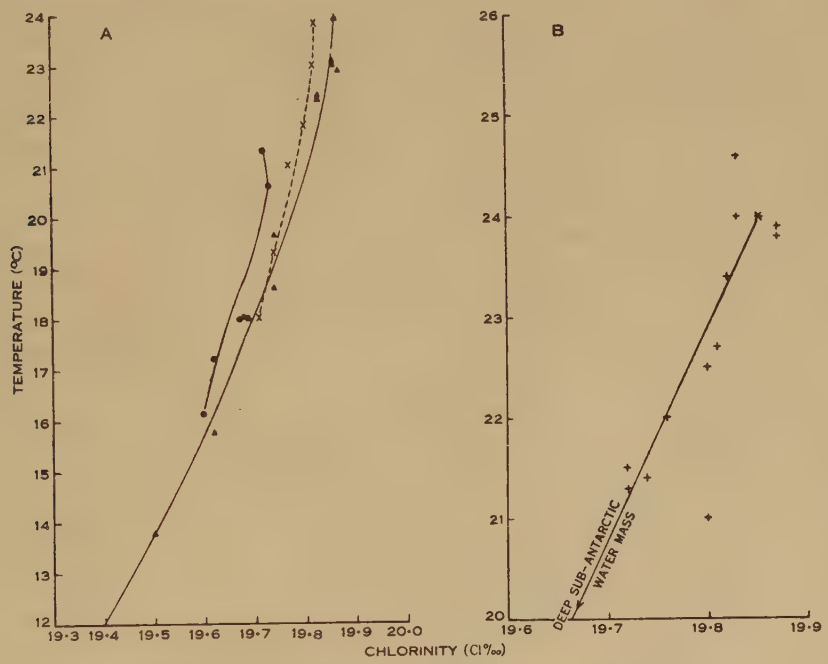

Fig. 7.—*A*, chlorinity-temperature relationships of east Australian shelf and slope waters in lat. 31° 51′ S., January 1942.

●——● Long. 152° 51′ E.
×– – –× Long. 153° 10′ E.
▲——▲ Long. 153° 20′ E.

B, relationships of the primary surface water mass (*) and locally derived and modified surface water masses (+) of the northern New South Wales coast and shelf waters in January 1942.

The geographical distribution of these surface water masses of eastern Australia in August 1940 and January 1941 is shown in Figure 9, with some extrapolation beyond slope regions to clarify the plotting.

In August 1940 the region south of latitude 35° S. was dominated by the Central Tasman water mass, in agreement with later, more detailed evidence (Section V(*b*)) of the seasonal cycle of this water mass. The Coral Sea, and a possible southern limit of the South Equatorial, water masses were found north of this latitude. Later evidence (Section V(*b*)) suggests that this distribution is brought about by a recession to the north of the previous summer circulation rather than a winter flow of the East Australian current.

In January 1941 the Central Tasman was found south of latitude 40° S., and the Coral Sea water mass dominated the slope region of New South Wales. Later evidence (Section V(*b*)) indicates that the Coral Sea water mass arrives off Sydney in October–December of each year, so that the 1941 distribution was probably its southernmost limit. The single occurrence of the South Equatorial water mass in January 1941 in latitude 32–33° S. agrees with later evidence (Section V(*b*)) about its seasonal characteristics and meandering distribution.

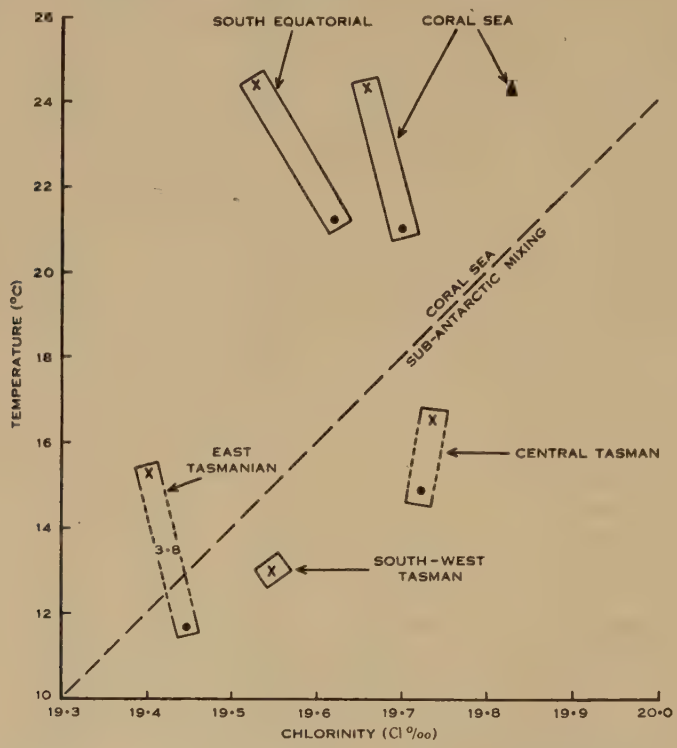

Fig. 8.—The primary surface water masses of the east Australian coast and shelf regions and their seasonal changes in chlorinity-temperature characteristics, August 1940–January 1942.
● August 1940. × January 1941. ▲ January 1942.

The isolated occurrences of the Central Tasman (30° S.) and of the South-west Tasman (36–39° S.) in coastal waters in January 1941 are linked with their more general distribution at intermediate levels.

(*b*) *The Regional Surface Water Masses of the Sydney–Wellington: Sydney–Auckland Regions of the Tasman Sea*

In this section the data utilized are from the upper 5 m of water and are therefore subject to greater adventitious effects of heating and cooling, evaporation, and precipitation than occur within a more representative column of greater depth. It has been possible to make some allowance for seasonal changes in temperature,

Fig. 9.—Distribution of the surface water masses of east Australian shelf and slope waters.

Water Mass	*A*. Aug. 1940		*B*. Jan. 1941	
	Cl (‰)	Temp. (°C)	Cl (‰)	Temp (°C)
South Equatorial	19·62	21·20	19·50	24·30
Coral Sea	19·71	21·20	19·67	24·40
Central Tasman	19·72	14·80	19·72	16·50
East Tasmanian	19·45	11·50	19·40	15·20
South-west Tasman	—	—	19·54	13·00

but not for evaporation-precipitation effects on chlorinity, in the separation and identification of seasonally occurring surface water masses in the region between Sydney and New Zealand. In the absence of a correction for these latter effects, it

is sometimes difficult to decide whether certain combinations of chlorinity and temperature are significant for this separation or merely seasonal changes in the same water mass. However, since the evidence from this section will be used mainly to indicate some general features of the seasonal cycle of surface water masses between Sydney and New Zealand, whose identity will be established from all the data of this paper, this limitation is not considered serious.

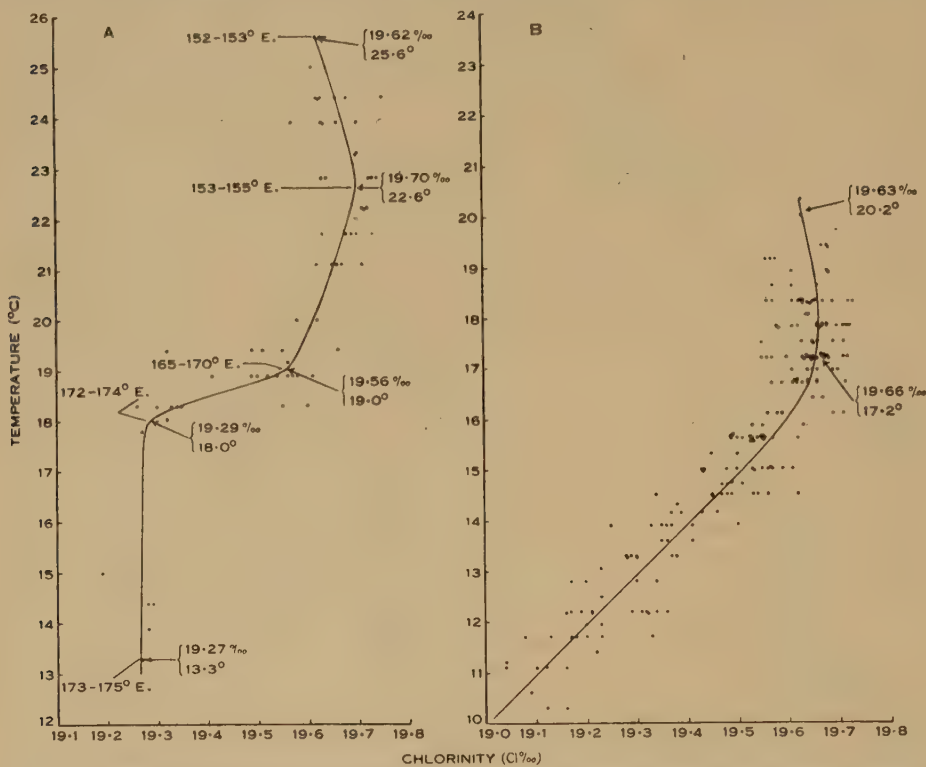

Fig. 10.—Chlorinity-temperature relationships of the surface Tasman Sea waters between Sydney and New Zealand. *A*, January 1953. *B*, July 1953.

From a series of conventional chlorinity-temperature diagrams for every month of the period 1953–1954, of which Figures 10*A* and 10*B* are examples, it has been possible to determine the regional water masses for each month. The scatter of these data, compared with that in a plot of the vertical chlorinity-temperature relationships at any fixed station (Fig. 11*A*), is due in part to the adventitious surface effects previously discussed, but also to a much less accuracy in the temperature than in the chlorinity values of the surface data. Figure 10*A* shows that in January 1953 the regional water masses were spaced geographically in the same relative order as in the chlorinity-temperature diagram. For this month therefore the majority of points on this diagram could have been formed by horizontal mixing between the regional water masses at the surface. In general it seems probable that, at the surface of the Tasman Sea, horizontal mixing between regional water masses can account for the majority of the observed chlorinity-temperature characteristics in

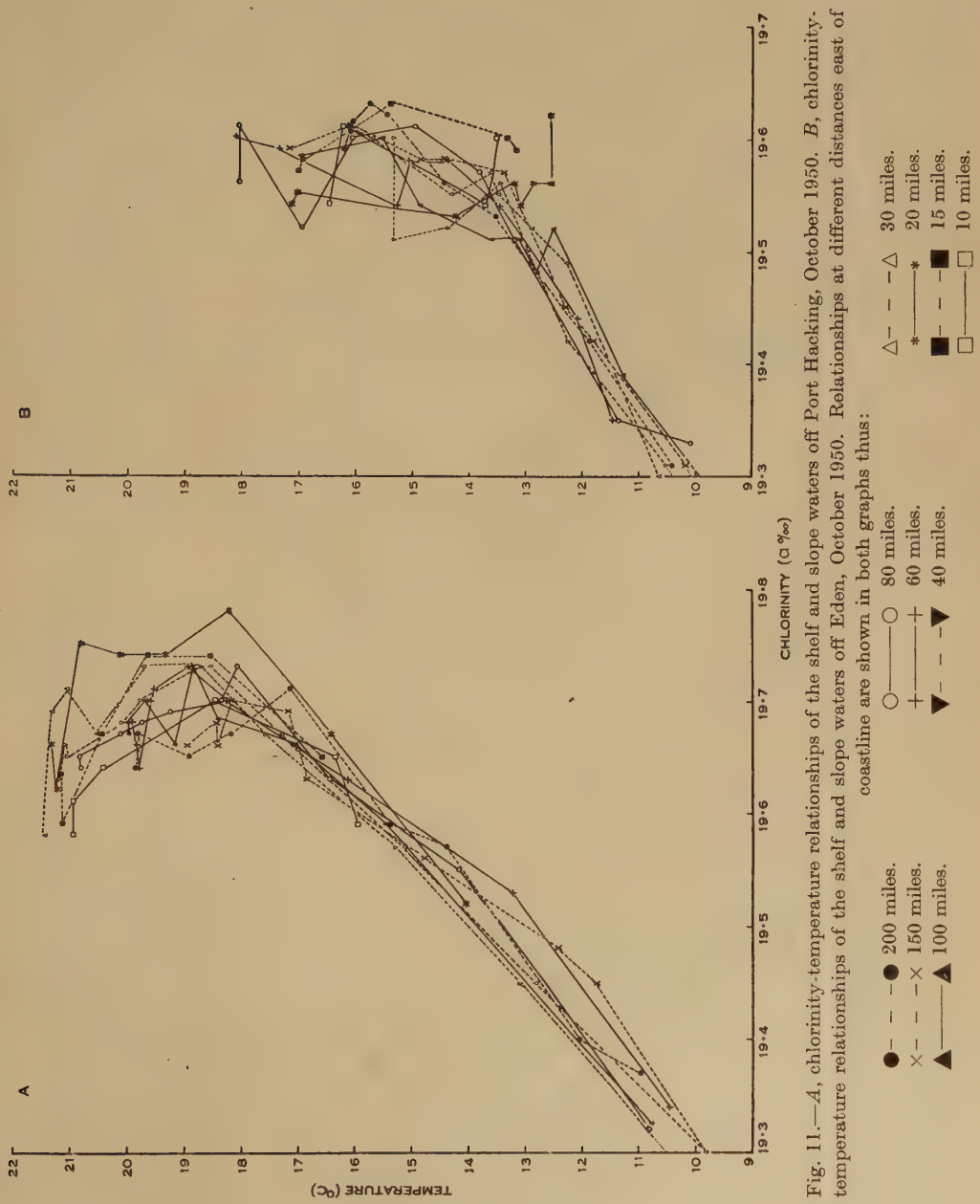

Fig. 11.—*A*, chlorinity-temperature relationships of the shelf and slope waters off Port Hacking, October 1950. *B*, chlorinity-temperature relationships of the shelf and slope waters off Eden, October 1950. Relationships at different distances east of coastline are shown in both graphs thus:

all months except June to September when some vertical mixing occurs. This assumption has been followed in the preparation of Figure 6, in which the degree of horizontal mixing has been indicated for 1954 data.

In both Figures 6 and 12 regions of vertical mixing have not been plotted and only such data as fit the assumption of horizontal mixing have been used. Both these figures therefore represent a simplification of the complete picture, which can only be drawn when more extensive data are available.

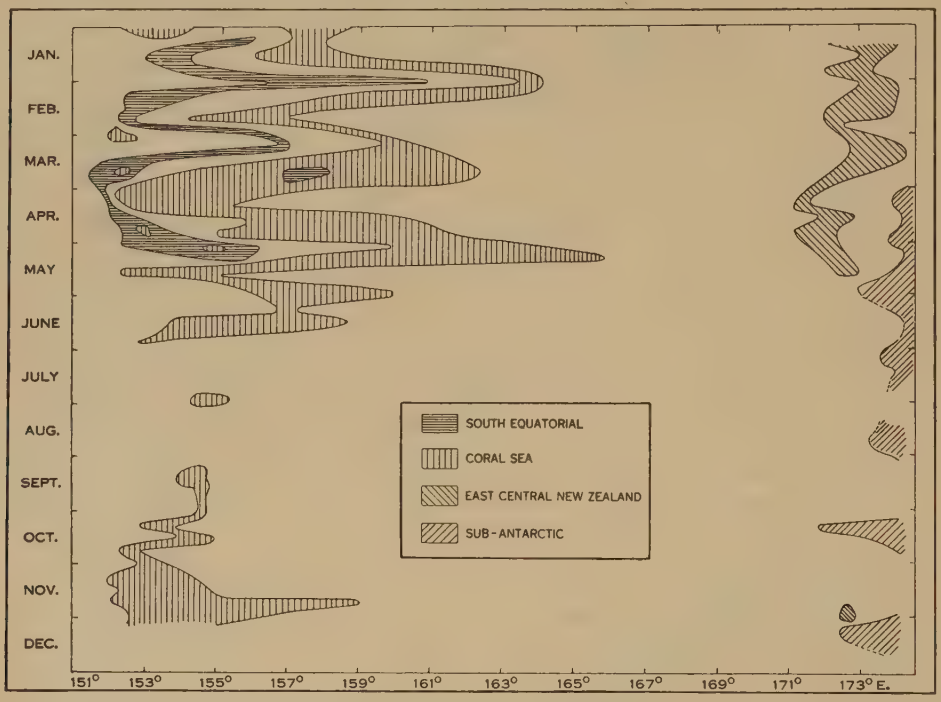

Fig. 12.—Seasonal distribution of the principal surface water masses along a section from Sydney to Wellington, 1953.

(i) 1953.—From the 1953 data it was possible to derive the seasonal cycle of certain important surface water masses of the Tasman Sea. Figure 12 shows that the East Australian current (Schott 1935) is composed of two water masses which reach their maximum development at different times of the late spring–summer period. The Coral Sea water mass first appears off Sydney in November; this could be associated with the December peak of flow of the current to the south shown in Figure 13, which was prepared from the British Meteorological Office records (Great Britain, Meteorological Office 1938). The South Equatorial water mass, on the other hand, does not appear off Sydney until late January or early February, and the maximum velocities in February of each year between latitudes 26° and 30° S. (Fig. 13) are considered to be associated with its southerly flow. It rarely occurs off Sydney after early May. The Coral Sea water mass is generally spread over a wide band and located at some distance from the coast. The South Equatorial water mass is variable in position and width. Sometimes it veers close to the coast and its width narrows.

Generally under these conditions it has a higher temperature. Figure 14 shows that the nearer this water mass approached the coast, and presumably therefore, the higher the degree of its canalization, the higher was its temperature. During its canalization its surface layers at least tend to undergo less mixing with adjoining water masses. Its original high temperature and relatively low chlorinity are thus better preserved during movement from its source.

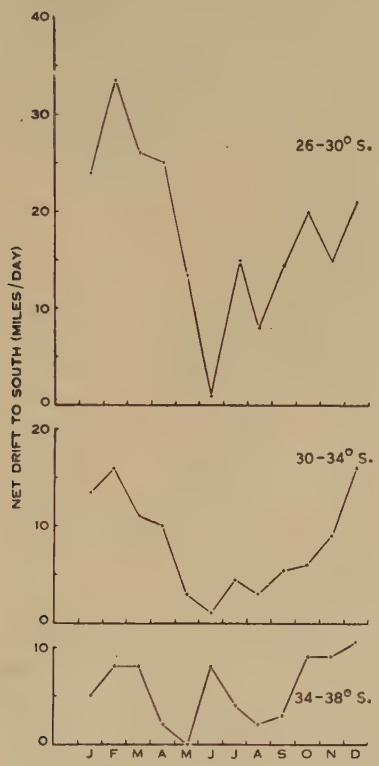

Fig. 13.—Daily net drift to the south of the east Australian current. Compiled from ships' drifts by the Marine Division of the Meterorological Office, London, 1938.

There is some association between the meandering of the South Equatorial and the zonal distribution of the Coral Sea water masses. Figure 6*B* indicates that in April 1954 a westerly flow of the Coral Sea water mass occurred. This may be the dynamic structure associated with these zonal changes in distribution. It is clear that the East Central New Zealand water mass occurs in the eastern side of the Tasman Sea only during the summer period, and that in the winter period this region is dominated by a water mass similar in chlorinity and temperature to surface Sub-Antarctic waters. The complete absence of the Central Tasman water mass from the 1953 Sydney–Wellington section could mean a more southerly distribution in that year. Because of lack of total phosphorus data in that year, certain chlorinity-temperature combinations could not be positively identified as Central Tasman and are not included in Figure 12.

(ii) 1954.—Because fewer values were available, the 1954 data from the Sydney–Auckland and Sydney–Wellington crossings of the Tasman Sea were grouped together. A series of charts was prepared showing the average monthly distribution of regional water masses within the area bounded by these crossings (Fig. 6).

Because of the time lag between these crossings each month, and of their wide separation at the New Zealand side, the boundaries of the water masses on these charts have been smoothed considerably. In 1954 the F.R.V. *Derwent Hunter* collected hydrological data in the south-western Tasman Sea (Section V(*c*)) and it has been possible to use these data to extend the southern limits of water mass boundaries in Figures 6*A* and 6*E*. The 1954 surface data have been used therefore to prepare general charts of the distribution of the Tasman Sea water masses.

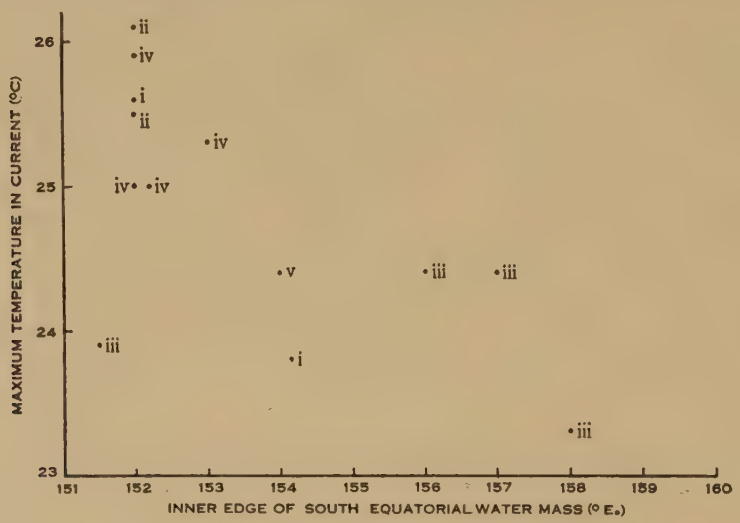

Fig. 14.—Temperature of the South Equatorial water mass in relation to the positioning of its inner edge. Roman numerals refer to the month of occurrence of the water mass off Sydney.

The seasonal cycle of these water masses was the same as for 1953, except that the Central Tasman water mass in 1954 occurred along and to the north of the Sydney–Wellington crossing. In 1954 this water mass was of major importance in the southern Tasman Sea between June and October. The tongue of this water mass in April (Fig. 6*B*) could be considered as the earliest indication of its autumn uncovering and southern movement. It is possible that absence of data from the southern Tasman Sea proper for this month may be over-emphasizing this feature.

In February 1954 (Fig. 6*A*) the South Equatorial water mass was 200 miles east of Sydney but only 100 miles east of Eden, some 200 miles to the south. In that month there was evidence of this water mass off the east coast of Tasmania and also 500 miles east of Eden. A bifurcation of flow in latitudes 38–40° S. had probably occurred.

In December 1954 (Fig. 6*E*) the western side of the Tasman Sea south of latitude 35° S. was dominated by the Coral Sea and the South-west Tasman water

masses. The Central Tasman was not found at the surface, and other evidence (Section V(*c*)(ii)) indicates that it was also absent from subsurface levels.

(*c*) *The Regional Surface Water Masses in the South-western Sector of the Tasman Sea between Latitudes* 34° *and* 44° *S. and Longitudes* 142° *and* 156° *E., including Bass Strait*

In 1954, autumn and midsummer surveys of the south-western Tasman Sea, including Bass Strait, were carried out by F.R.V. *Derwent Hunter*. Although some 6–8 weeks were necessary for each survey it is proposed to consider the region as a unit (Fig. 1), and the data as synoptic.

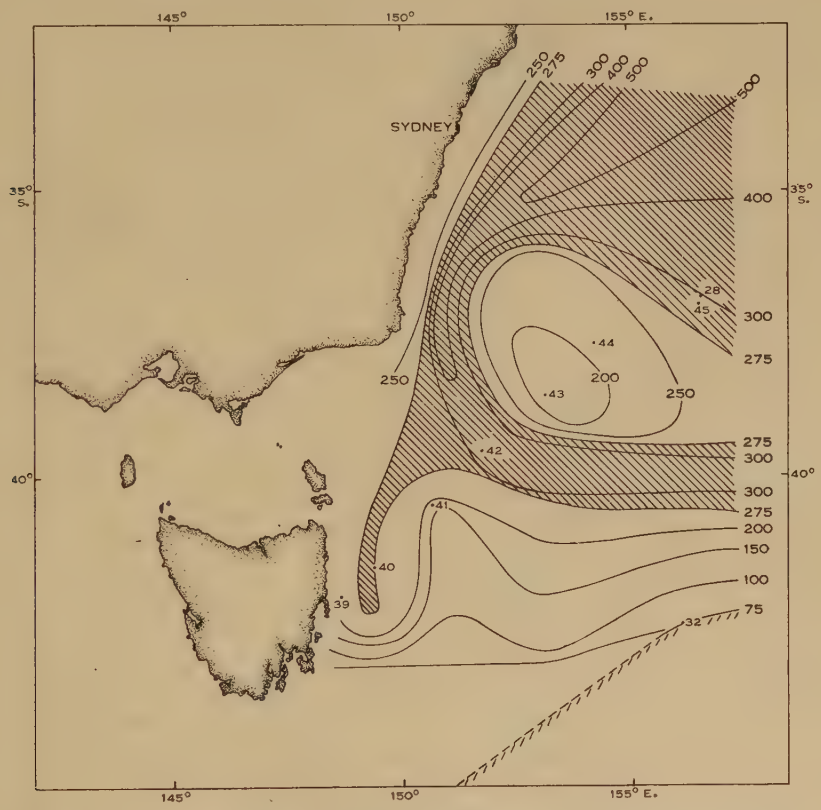

Fig. 15.—Depth in metres of the 12°C isotherm in the south-west Tasman in February 1954. Hatching indicates depth below 275 m. The numbers extending north-east from Tasmania refer to station positions, from which the chlorinity-temperature data of Fig. 16*A* were obtained.

(i) *February–March* 1954.—Two cruises were made in the autumn, one in February, for which temperatures alone are available except for stations 28, 32, and 39–45/54 (Fig. 15), and the other in March, for which temperature, chlorinity, and total phosphorus data are available for all stations. The results of the March cruise are considered first.

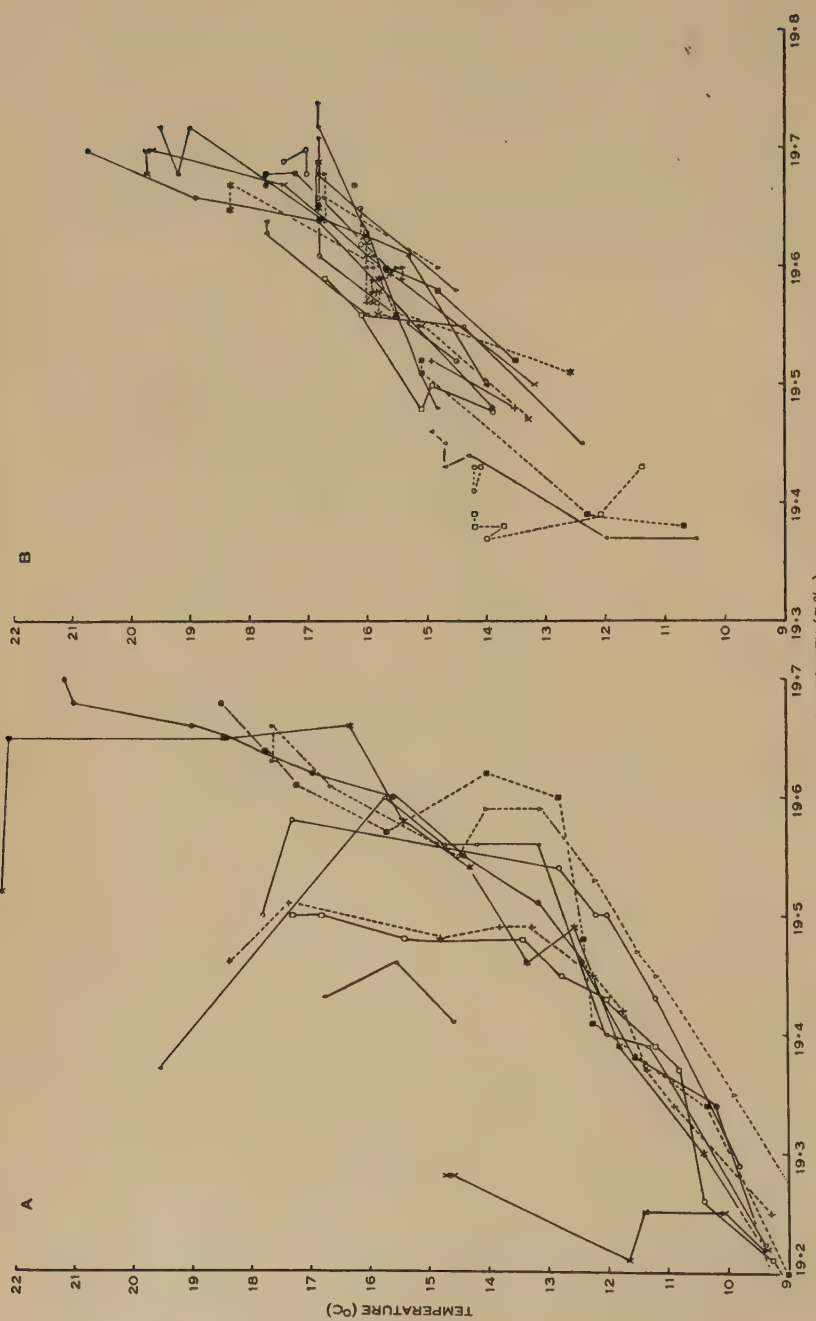

Fig. 16.—*A*, chlorinity-temperature relationships of the south-west Tasman waters, February 1954.

● —— ● 28/54 × —— × 32/54 ▲ —— ▲ 38/54 ■ - - - - ■ 39/54 ▽ - - - - ▽ 40/54 □ —— □ 41/54
○ —— ○ 42/54 + - - - + 43/54 △ —— △ 44/54 * —— * 45/54

B, chlorinity-temperature relationships of Bass Strait waters, March 1954.

● —— ● 51/54 × —— × 52/54 ▲ —— ▲ 53/54 ■ —— ■ 54/54 △ —— △ 55/54 □ —— □ 57/54
+ —— + 58/54 ○ —— ○ 59/54 ▽ —— ▽ 60/54 ▼ —— ▼ 61/54 * —— * 62/54 ⊙ —— ⊙ 66/54
× - - - × 69/54 ▲ - - - ▲ 71/54 ■ - - - ■ 72/54 △ - - - △ 73/54 □ - - - □ 74/54 + - - - + 83/54
○ - - - ○ 75/54 ▽ - - - ▽ 82/54 ▼ - - - ▼ 83a/54 ⊙ - - - ⊙ 85/54 ⊡ - - - ⊡ 87/54 * - - - * 88/54

(1) *Bass Strait and Approaches* (*March* 1954).—The chlorinity-temperature relationships of the data from this region in March 1954 are given in Figure 16*B*. From these relationships the surface water masses of Table 7 have been identified.

TABLE 7

REGIONAL SURFACE WATER MASSES OF BASS STRAIT AND ITS APPROACHES, MARCH 1954

Location of Water Mass	Chlorinity (‰)	Temp. (°C)	Mean Total P (μg/l.)
North-eastern Bass Strait	19·73	16·80	10 (8–14)*
Eastern Bass Strait	19·72	19·50	11 (10–12)*
East and west Tasmanian coasts	19·43	14·20	15 (14–17)*

*Range of values within water mass.

Figure 17 shows the distribution of these surface water masses in Bass Strait in March 1954. The high-chlorinity water in the north-eastern region could be the Central Tasman water mass, but it is considered more likely that it is an eastward

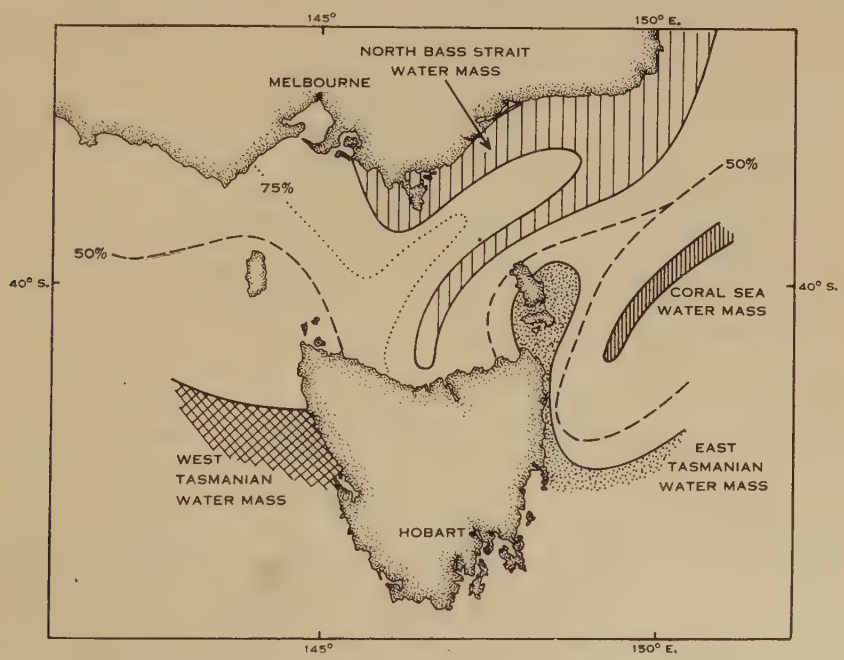

Fig. 17.—The surface water masses of Bass Strait, March 1954.

extension of the North Bass Strait water mass which was found in November 1954 (Section V(*c*)(ii)) in the north-western approaches of Bass Strait. The North Bass Strait water mass is continuous with the high-chlorinity gulf waters of South

Australia. It is considered unlikely that the Central Tasman water mass could be found in summer in the vicinity of the north-eastern approaches of Bass Strait.

(2) *South-west Tasman* (*February* 1954).—The chlorinity-temperature relationships for this region are plotted in Figure 16*A*. From these the regional water masses of Table 1 have been identified. Figure 16*A* shows that subsurface water masses were modifying the linear mixing relationship between a surface water mass of chlorinity 19·70‰ and temperature 21·2°C and a deep Sub-Antarctic water mass

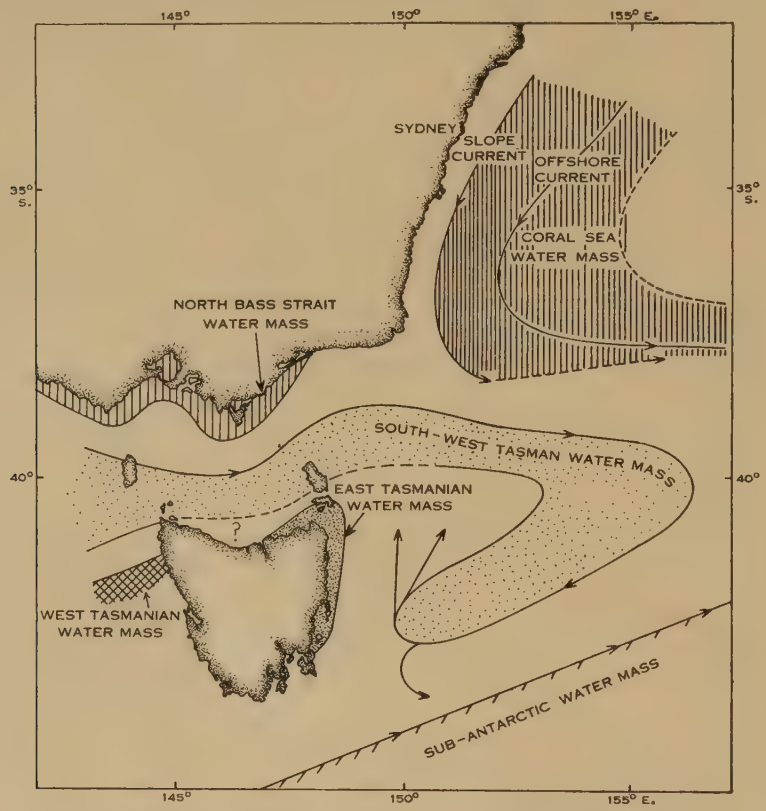

Fig. 18.—Distribution of the principal surface water masses of the south-west Tasman and Bass Strait, November–December 1954.

whose upper limit had chlorinity and temperature values of 19·32‰ and 10·5°C. Particularly at station 39/54, there is evidence of an intermediate water mass of chlorinity 19·60‰ and temperature between 13° and 14°C. This water mass is possibly identical with the South-west Tasman water mass, which as shown in Section VI is found in the eastern approaches of Bass Strait in winter, but in early summer lies to the north and north-east of Tasmania in latitudes 39–40° S. and apparently curves back towards Tasmania in about latitude 42° S. (Fig. 18).

Insufficient chlorinity data are available for this cruise to plot the distribution of water masses, but if the bathymetry of the 12°C isotherm is plotted (Fig. 15) a separation into regions influenced by a northern warm and a southern cold water mass

can be shown. The trough of warm water extending from wide offshore in latitude 34° S. to slope waters in latitude 38° S. and thence eastwards to latitude 40° S. is the probable path of the southerly-flowing warm water mass. The bifurcation of flow of this water mass and an extension of its flow along the east Tasmanian coast is based upon data from station 40/54 only. There is sufficient evidence from seasonal studies of hydrological properties of coastal stations in this region to indicate that this diversion of flow occurs in some summers.

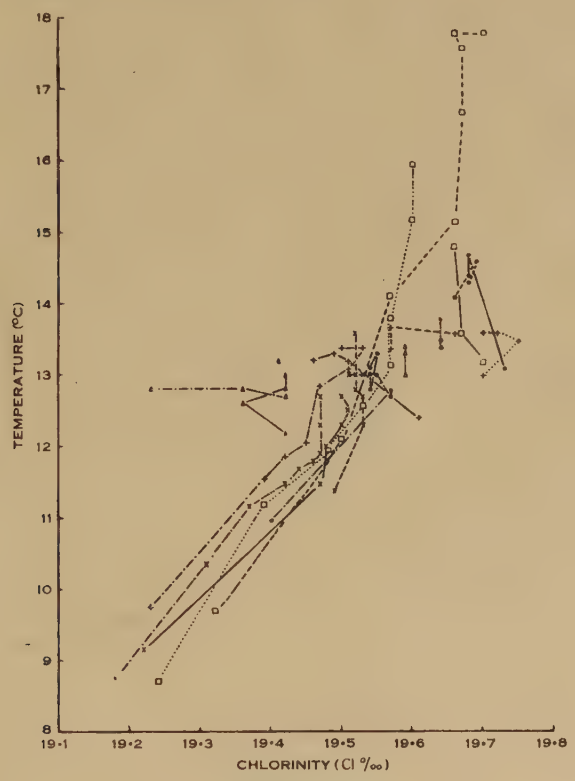

Fig. 19.—Chlorinity–temperature relationships of Bass Strait waters, November 1954.

Stations:

123 ●——● 126 ●....● 128 ●---● 129 ●-·-·●
130 ×---× 131 ×——× 132 ×-·-·× 133 ×....×
136 △--△ 141 △ 142 △-·-·△ 143 △——△
144 +-·-·+ 146 +——+ 148 +---+ 149 +....+
152 □——□ 155 □---□ 157 □ — — □

The surface chlorinities and temperatures at stations 43/54 and 44/54 (Fig. 16*A*) were probably caused by mixing between the waters at station 45/54 and the warmed Sub-Antarctic waters of station 32/54. This would indicate that prior to February 1954 the trough of warm water, centred along latitude 40° S. (Fig. 15), lay to the north of station 44/54.

In the absence of chlorinity data for the whole region the water mass identifications for this cruise are incomplete, but a probable summer limit of heating of the Sub-Antarctic and further evidence of the intermediate depth distribution of the South-west Tasman in summer have been obtained.

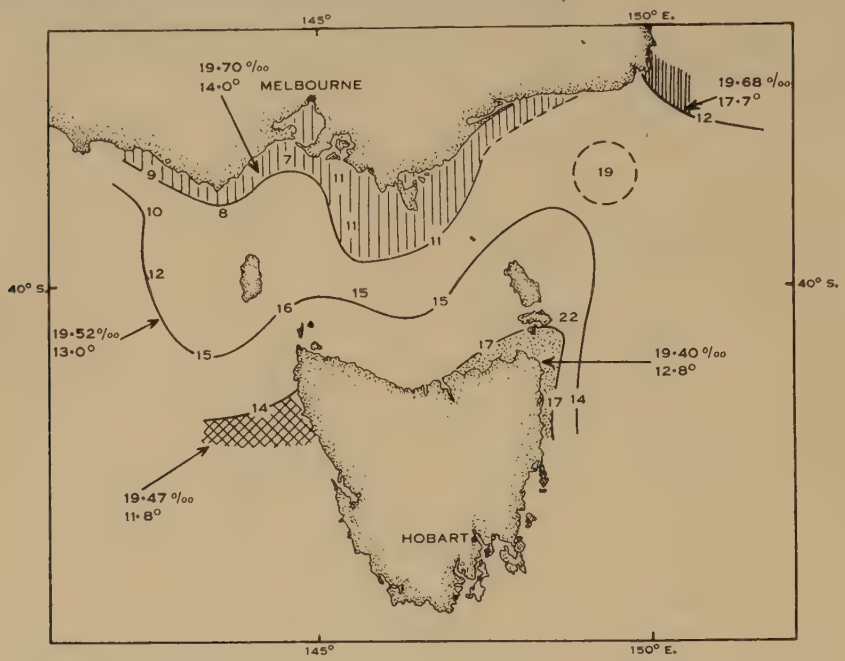

Fig. 20.—Surface water masses (Table 8) and the mean upper 50 m total phosphorus content (μg/l.) of Bass Strait waters, November 1954.

(ii) *November–December* 1954. (1) *November* 1954.—Using the chlorinity-temperature relationships of Figure 19, the dominant water masses in Bass Strait

TABLE 8

REGIONAL SURFACE WATER MASSES OF BASS STRAIT AND ITS APPROACHES, NOVEMBER 1954

Location of Water Mass	Chlorinity (‰)	Temperature (°C)	Mean Total P (μg/l.)
Southern N.S.W. coast	19·68	17·70	12*
North coast of central Bass Strait	19·70	14·00	10 (7–11)†
West Tasmanian coast below 42° S.	19·47	11·80	14*
North-east Tasmanian coast	19·40	12·80	19 (17–22)†

*One station only.

†Range of values within water mass (Fig. 2*D*).

and its approaches in November 1954 were determined (Table 8). The surface distribution of these water masses and their total phosphorus content are plotted

in Figure 20. From this chart the mean total phosphorus of the water masses in Table 8 were determined.

The southern New South Wales water mass is considered to be the residuum of the Central Tasman water mass occupying the eastern approaches to Bass Strait in midwinter, rather than of Coral Sea origin. The north-eastern Tasmanian water mass is considered identical with the East Tasmanian water mass already described (Section V(*a*)).

The water mass along the north coast of central Bass Strait was characterized by high chlorinity, low temperature, and a mean total phosphorus of 10 μg/l. This is considered identical with the north-eastern Bass Strait water mass in March 1954, and as discussed later (Section V(*d*)(i)), is probably continuous with western Victorian and South Australian waters. The slight increase in total phosphorus from west to east (Fig. 20) could be interpreted as an effect of increased bottom sediment load during the eastward movement of this water mass through the shallow and turbulent Bass Strait region.

The waters occupying the central zone of Bass Strait (chlorinity 19·52‰, temperature 13°C; Fig. 20) are considered to be a westward extension of the South-west Tasman water mass of eastern Tasmania.

This conclusion has been arrived at on the evidence of this cruise, and also from the seasonal cycle of surface chlorinities and temperatures along the *Taroona* section (Fig. 21), which is discussed later (Section V(*c*)(iii)).

From the same evidence it has been concluded that the coastal water mass in north-eastern Tasmania (Fig. 20) was formed by riverine dilution along the north coast of Tasmania, in the spring, of the waters of the central zone of Bass Strait.

It is impossible to decide whether the coastal waters of eastern and western Tasmania both originate in this region.

(2) *December* 1954.—For the December 1954 data chlorinity, temperature, and total phosphorus were used to distinguish the various surface water masses occupying the south-western Tasman sector. Table 4 lists the properties of the various water masses in the south-western sector in December 1954. Figure 18, covering the region surveyed in November and December as a whole, shows how the surface water masses of the region were distributed and their probable paths of movement.

In this figure an easterly flow through Bass Strait is indicated for November–December 1954. This is based upon the evidence previously discussed. If the easterly transport of such a flow was considerable and persisted for a sufficient time, waters of the region west of Tasmania might conceivably affect the water-mass structure of the south-western Tasman Sea. However, because of the shallowness of Bass Strait (Fig. 2) and the slow rate of seasonal movement of its waters indicated by the March and November distribution of the North Bass Strait water mass (Figs. 17, 18), no account has been taken of this possibility. Moreover it has been impossible to detect an effect of the North Bass Strait water mass upon oceanic conditions in the eastern approaches, despite its seasonal movement through the northern part of that region. Figure 22 shows how the various water masses of Bass Strait and its approaches were related in 1954 to those of the Tasman Sea (Table 2). It is evident that the Bass

Strait water masses were similar to those of the Tasman Sea as a whole, except for the North Bass Strait water mass.

In December 1939 F.R.V. *Warreen* occupied a series of stations from Bass Strait to the gulfs of South Australia. The chlorinity-temperature relationships of data from these stations are shown in Figure 23, which also gives the chlorinity-temperature characteristics of waters at the entrance to St. Vincent's Gulf (*gulf*

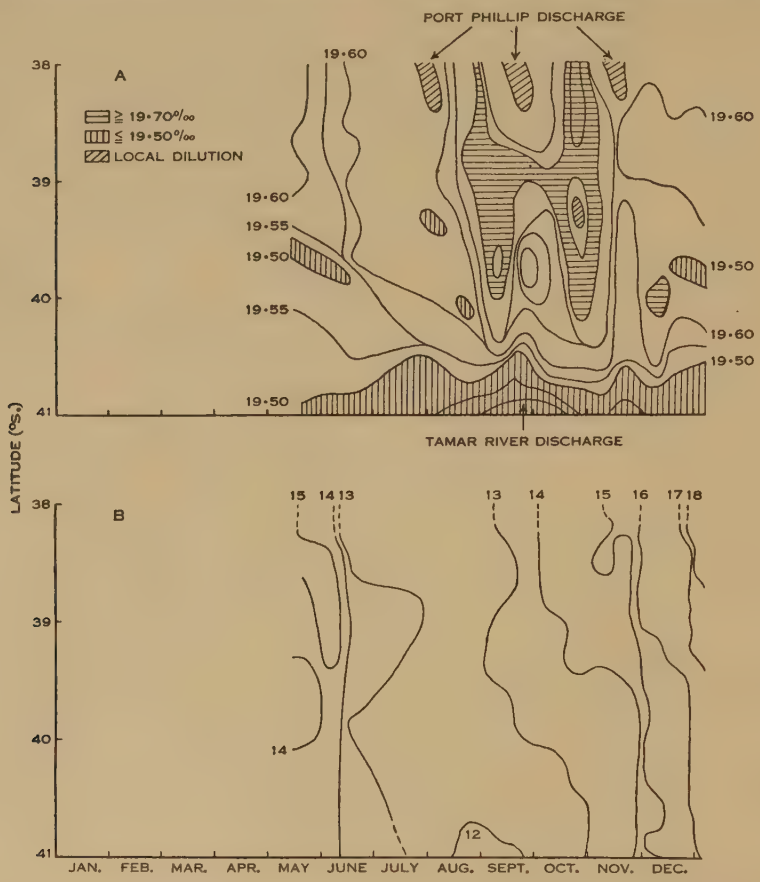

Fig. 21.—*A*, surface chlorinity isopleths across a section of Bass Strait from Port Phillip to Low Head, 1954. *B*, surface temperature isopleths across a section of Bass Strait from Port Phillip to Low Head, 1954.

water, Fig. 23). It seems reasonable to assume that at depths between 30 and 100 m there is a movement to the east of a high-chlorinity water mass, originating in the gulf region of South Australia. This high-chlorinity water mass is considered the source of the North Bass Strait water mass which was found in Bass Strait in March and November 1954. However, until this continuity is fully established the latter will be referred to as the North Bass Strait water mass.

(iii) *Seasonal Changes in the Surface Water Masses of a Section from Port Phillip Heads to Low Head, Bass Strait, during* 1954.—In May 1954 surface sampling from

T.S.S. *Taroona* was commenced during her regular passage from Melbourne to Launceston (Fig. 1).

The seasonal chlorinity distribution (Fig. 21*A*) demonstrates that the chlorinity in the May–August period is less than 19·60‰ for the greater part of the section, with chlorinities below 19·40‰ along the north Tasmanian coast. This distribution supports the idea of a westerly movement of the South-west Tasman water mass into

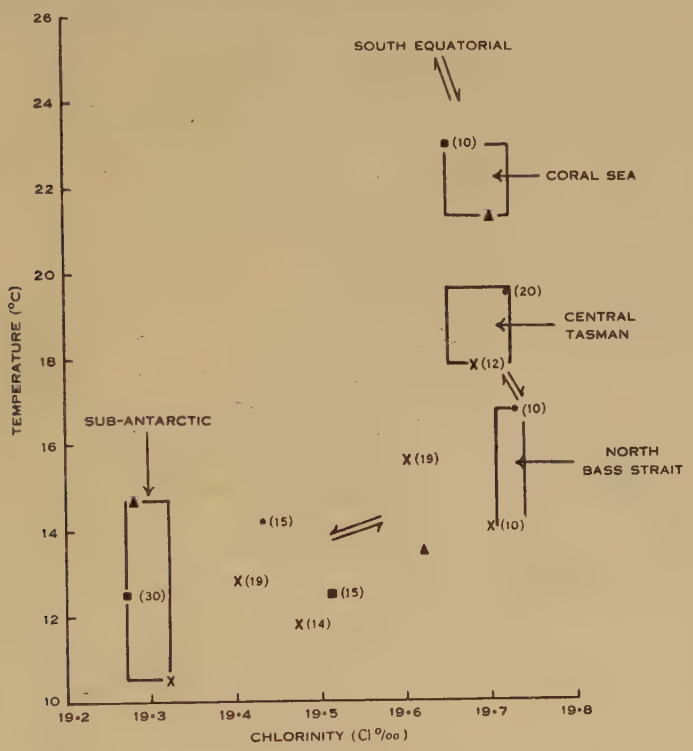

Fig. 22.—Interrelationships of the surface water masses in Bass Strait and the south-west Tasman Sea in the periods February–March and November–December 1954. The figures in brackets are the mean total phosphorus content (μg/l.).

● Bass Strait, March 1954.
× Bass Strait, November 1954.
▲ South-west Tasman, February 1954.
■ South-west Tasman, December 1954.

Bass Strait during this period. In September and October a high-chlorinity, low-temperature water mass—presumably the North Bass Strait water mass (Fig. 20)—dominated the greater part of this section, but by November chlorinities less than 19·60‰ and temperatures, in the southern half of the section, of less than 14°C support the suggestion in Section V(*c*)(ii) that during this period an easterly movement of the South-west Tasman water mass occurred in the southern region of Bass Strait.

The southern end of this section is dominated by water with chlorinities less than 19·50‰, and the northern distribution of these waters is at a maximum in the

months July–September. This is considered the period of formation of the Tasmanian coastal water mass.

(iv) *Investigations of R.R.S.* Discovery II *in South-eastern Australian Waters in October* 1950.—Figure 11*A* shows the chlorinity-temperature relationships of data from a Port Hacking section, and Figure 11*B* those from an Eden section, worked

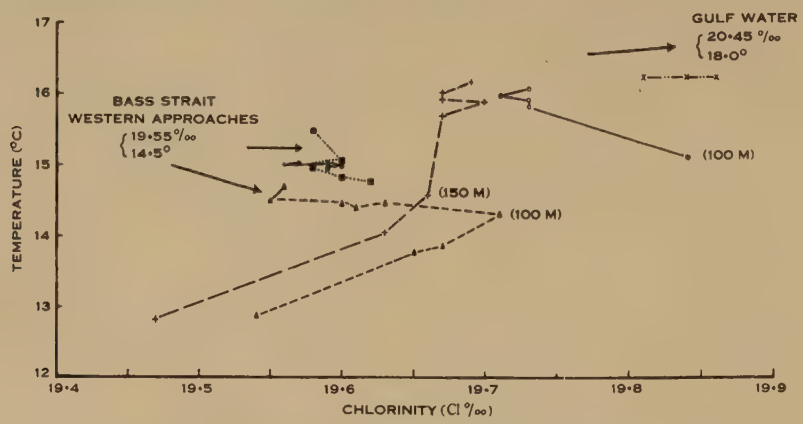

Fig. 23.—Chlorinity-temperature curves for F.R.V. *Warreen* stations in South Australian and Victorian coastal waters, December 1939.
● 313/39. ○ 331/39. × 342/39. ▲ 343/39. ■ 344/39. + 345/39.

by R.R.S. *Discovery II* in 1950. Table 9 lists the dominant surface and intermediate water masses deduced from these relationships.

A comparison of these chlorinity-temperature relationships shows that a deep intermediate water mass with a chlorinity of 19·62‰ and a temperature of 12·5°C was influencing considerably the onshore slope waters off Eden between 100

TABLE 9
REGIONAL WATER MASSES OFF EDEN AND PORT HACKING, OCTOBER 1950

Location of Water Mass	Chlorinity (‰)	Temperature (°C)	Total P (μg/l.)
Northern surface offshore water mass	19·65	20·70	10–12
Northern intermediate water mass	19·72	18·60	18–20
Southern surface offshore water mass	19·59	18·00	12–15
Southern intermediate water mass	19·62	12·50	20–25

and 200 m. For comparable chlorinity values off Port Hacking the temperatures were several degrees higher and the influence of this deep intermediate water was apparently much less.

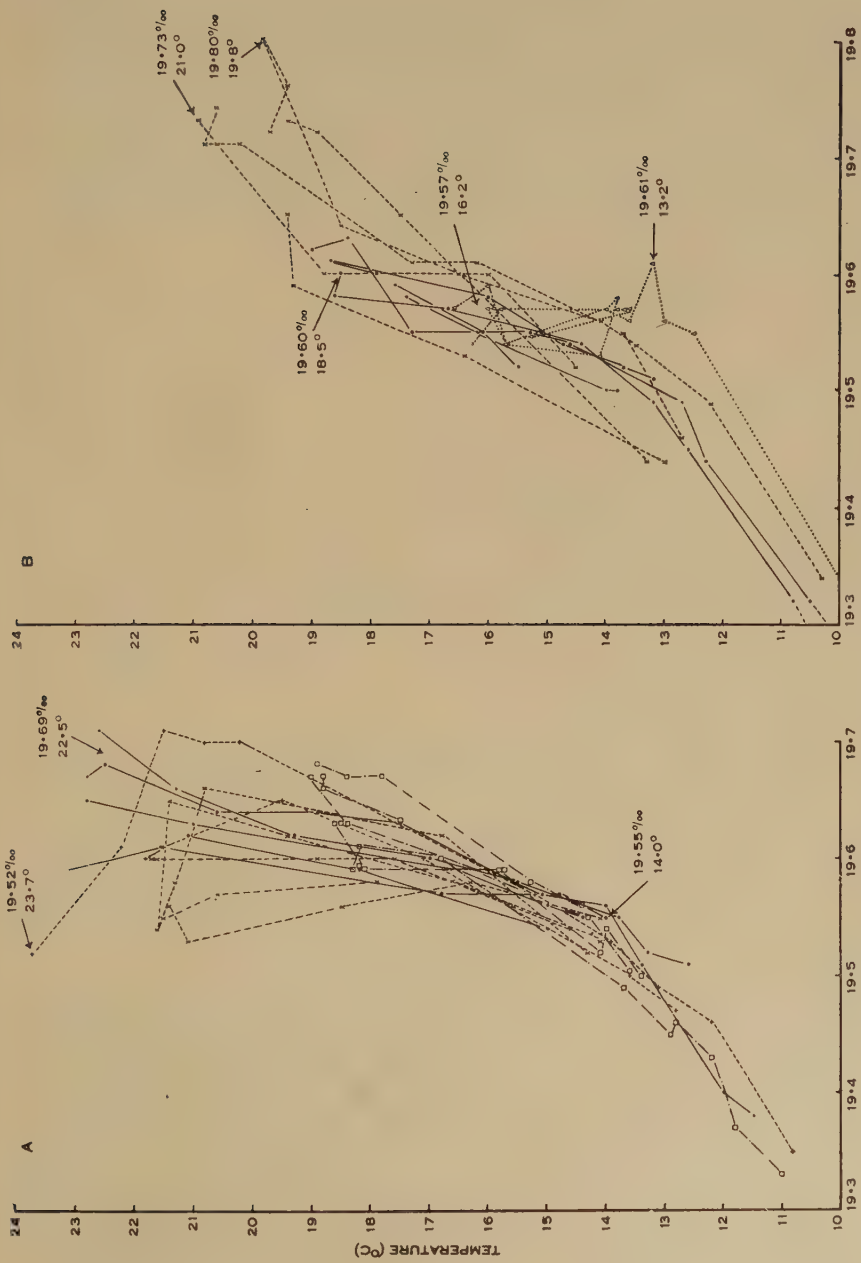

Fig. 24.—*A*, chlorinity-temperature relationships of shelf and slope waters off Port Hacking.
●——● Stations occupied in February 1953. ×——× Early April 1953.
+——+ Late April 1953. □—·—·□ November 1953.
B, chlorinity-temperature relationships of shelf and slope waters off Eden.
●——● Stations occupied in January 1953. ×– – –× March 1953. △- - - - - -△ November 1953.

This intermediate water mass was most strongly developed in the western end of the section off Eden and had chlorinity, temperature, and total phosphorus characteristics very similar to those of the South-west Tasman water mass occurring at the surface off eastern Tasmania in December 1954 (Table 4). It is possible that in October 1950 some of the South-west Tasman water mass had moved north of the path followed in December 1954 and had sunk and spread at an intermediate level. The much lower chlorinities and temperatures of the surface water masses off Eden, compared with those off Sydney in October 1950, suggest that the South-west Tasman water mass may also have been present at an earlier period of the year as a surface-dominant water mass. The northern intermediate water mass was probably connected with the winter flow of the Central Tasman water mass into the south-western Tasman Sea.

TABLE 10

REGIONAL SURFACE WATER MASSES OF SOUTH-EASTERN AUSTRALIAN SHELF AND SLOPE WATERS, 1953

Location of Water Mass	Chlorinity (‰)	Temperature (°C)
Offshore surface water mass, Sydney, February	19·69	22·50
Offshore surface water mass, Sydney, April	19·52	23·70
Intermediate water mass, Sydney, January and November	19·55	14·00
Offshore surface water mass, Eden, January	19·60	18·50
Slope surface water mass, Eden, March	19·73	21·00
Offshore surface water mass, Eden, March	19·80	19·80
Intermediate water mass, Eden, March	19·61	13·20
Surface water mass, Eden, November	19·57	16·20

In a previous paper dealing with these data Rochford (1952) was of the opinion, from a distribution of density, that little southern movement of surface water masses was occurring at this time off Port Hacking. Garner (1954), from thermograph records at about the same time, has found evidence of such a movement. He considers that the section was worked in the southern limit of the water masses advancing from the north and that rapid short-period changes in the circulation pattern could explain this discrepancy.

(v) *Coastal Sampling by H.M.A.S.* Warrego *and* Barcoo *in South-eastern Australian Waters during* 1953.—Figure 24*A* shows the chlorinity-temperature relationship of shelf and slope waters off Port Hacking in various months of 1953, and Figure 24*B* similar data off Eden in the same year. Table 10 gives the dominant water masses of south-eastern Australian shelf and slope water deduced therefrom.

The high-chlorinity surface water mass off Sydney in February was probably part of the flow of the Coral Sea water mass. The low-chlorinity surface water mass off Sydney in April, on the other hand, was probably part of the South Equatorial water mass. These water masses were still within the region influenced by coastal drainage, and lowered chlorinity values in April could be due to such effects. The *Wanganella* data (Fig. 12) show how the South Equatorial water mass moved onshore in March and April of 1953, so that the original explanation is probably correct.

The intermediate-level water mass which was weakly developed off Sydney in January and November 1953 was probably a northern extension of the intermediate-level water mass off Eden in March of the same year. On temperature and chlorinity characteristics alone, this intermediate-level water mass could be considered the same as the South-west Tasman water mass (Section V(*c*)(ii)). If this is so, then this water mass was detected in October 1950 (Table 9) and in March 1953 (Table 10) at intermediate levels in the waters off the southern New South Wales coast, at intermediate levels off eastern Tasmania in January 1941 (Table 5*B*), and at the surface in the same area in December 1954 (Fig. 18). Apparently in early summer in most years it sinks to intermediate levels and spreads over a considerable area of the south-western Tasman Sea before being absorbed into the summer system of water masses along the east Australian coast.

VI. The Source Regions and Nomenclature of the Surface Tasman Sea Water Masses

In this Section, the evidence given in previous Sections on the probable source regions of the surface water masses of the Tasman Sea is summarized and collated, and a system of nomenclature proposed.

In Section IV it was shown that in 1874 and 1908 a water mass with chlorinities greater than 19·90‰ and temperatures 22–24°C was to be found at levels between 100 and 200 m in the northern Coral Sea. From this and later evidence it is clear that such a water mass is a persistent feature of this region, which may thus be considered as the source of the high-chlorinity, high-temperature water mass flowing to the south off Sydney in October to May of most years. This is therefore called the Coral Sea water mass.

It was also shown in Section IV that a low-chlorinity (<19·40‰), high-temperature (>25°C) water mass was a persistent feature of the same region during the period 1874–1908. This was considered part of the South Equatorial flow into this region and its source region is well known. The water mass with chlorinities less than 19·60‰ and temperatures greater than 24°C occurring off Sydney in February to May of most years is considered part of the circulation of these South Equatorial waters and is named accordingly.

The low-chlorinity (<19·30‰), low-temperature (<14°C) water mass in the surface layers of the southern Tasman Sea (Section V(*c*)(ii)) and western New Zealand waters (Section V(*b*)) is considered continuous with the surface waters of the Southern Ocean and is accordingly called the Sub-Antarctic water mass. However, below certain depths, in the Tasman and Coral Seas, Sub-Antarctic waters which have sunk at the subtropical convergence and moved north at these intermediate levels are also found. These waters have a much more restricted range of properties. Deacon's (1937) values of chlorinity 19·32‰ and temperature 10·5°C characterize their upper boundary in the Tasman Sea.

At various locations and depths in the southern and central Tasman Sea there has been detected a water mass with chlorinities greater than 19·70‰ and temperatures 15–20°C. This water mass occurs off Sydney between June and December (Section V(*b*)). Since it has a high chlorinity it cannot be formed by mixing between

the Coral Sea and Sub-Antarctic water masses (Figs. 8, 22) which are present in the southern Tasman Sea in late autumn. For the same reason it cannot be formed from the low-chlorinity South Equatorial water mass. It is therefore considered that this water mass is formed by the cooling and sinking of surface Coral Sea water in the central Tasman Sea in the spring of each year. Its early summer distribution at intermediate levels (Section V(*a*)(ii)) supports this suggested mode of formation. Schott (1935) shows a tropical convergence extending north-east from latitude 37° S. and longitude 150° E., and this is considered the site of sinking and formation of this water mass. It is accordingly called the Central Tasman water mass.

The water mass with chlorinities between 19.50 and 19.60‰ and temperatures between 12° and 15°C, occurring in Bass Strait and off eastern Tasmania at the surface (Section V(*a*)(ii), V(*c*)(i),(ii)), and at intermediate depths along the southern New South Wales coast (Section V(*c*)(v)), is thought to originate in the eastern approaches of Bass Strait by mixing between Central Tasman and the deep Sub-Antarctic water. This water mass has been termed the South-west Tasman.

The origin of the North Bass Strait and of the Tasmanian coastal water masses in relation to their nomenclature has already been discussed (Section V(*c*)(ii), (iii)).

The low-chlorinity (19·10–19·30‰) and moderate-temperature (15–20°C) waters off the west coast of the North Island of New Zealand in the summer (Section V(*b*)(i), (ii)) could be formed by local riverine dilution of high-chlorinity waters. However, its area of distribution in relation to the size of the coastal rivers along this coast and its temperature characteristics do not favour such an origin. It is more probable that this water mass originates by spring and summer heating of Sub-Antarctic waters. The subtropical convergence is located farther north on the east than on the west coast of New Zealand, and Sub-Antarctic waters are often found on the Chatham Rise when tropical conditions prevail in the Tasman Sea at the same latitude. Because of this the Chatham Rise region has been favoured as the site of formation of this water mass and it has been named the East Central New Zealand.

VII. Some General Features of the Circulation of the Surface Tasman Sea Water Masses

From a study of the seasonal distribution of the various surface water masses of the Tasman Sea in relation to their source regions (Section VI), charts showing average summer and winter surface circulation have been prepared (Fig. 25).

The source region of the Coral Sea water mass is some 1200 nautical miles from Sydney. At the average spring velocity of 15 miles per day (Fig. 13), it would have to move from its source region in July–August to arrive off Sydney in October. This water mass is found off Sydney to distances of 600 miles offshore, probably in association with drifts to the east (Section V(*b*)(i)), but its average width would be about 400 miles. It disappears from the waters off Sydney in June–July, generally in association with a coastal tongue of the Central Tasman water mass (Fig. 9*A*), presumably moving northward.

The South Equatorial water mass is shown (Fig. 25*B*) as flowing through the region between New Zealand and New Caledonia. This path of entry is some 1000

nautical miles from Sydney, so that at an average summer velocity of 25 miles per day, this water mass would have to enter the Tasman Sea in December or January to arrive off Sydney in February. In its passage along the east Australian coast this water mass meanders within a strip 400 miles to the east of the coastline, and varies considerably in its width and depth. Figure 15 shows a considerable temperature increase down to 500 m, east of Sydney, which was probably associated with the flow of the South Equatorial water mass.

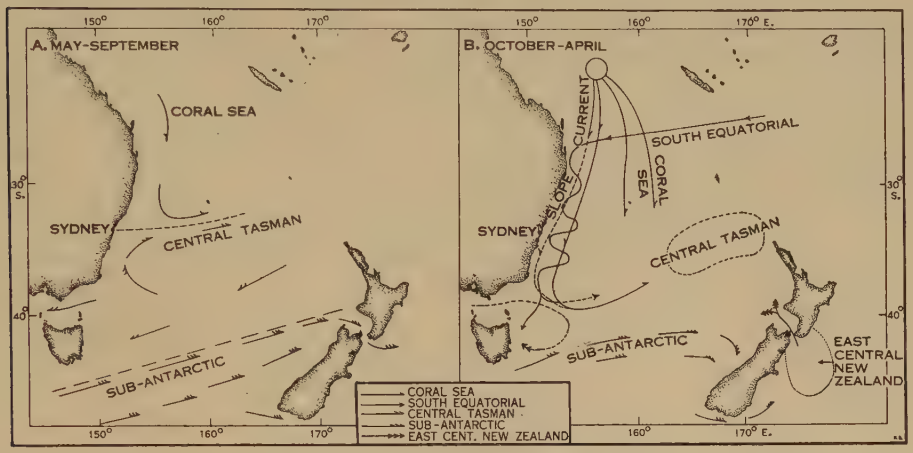

Fig. 25.—Probable paths of movement of the surface water masses of the Tasman Sea, based upon surface data only for the greater part of the region. *A*, May–September. *B*, October–April.

The Central Tasman water mass forms in the late spring period by sinking of the Coral Sea water mass (Section VI). Although its winter distribution is known only for the slope regions of south-eastern Australia (Section V(*a*)(i), (ii)), and for the *Wanganella* sections between Sydney and New Zealand (Section V(*b*)(i), (ii)), it is considered to be the major winter water mass of the Tasman Sea between 35° and 40° S. Because it originates at subsurface levels its winter distribution could possibly be due just as much to a recession to the north of the lighter overlying tropical waters, as to its actual movements from its origin. The circulation paths of this water mass shown in Figure 25 are therefore probably a combination of both vertical and horizontal flow.

The South-west Tasman water mass is considered to originate by vertical mixing between the Central Tasman water mass and subsurface Sub-Antarctic waters in the vicinity of the eastern approaches of Bass Strait, as the Central Tasman water mass moves west through this region in early winter. When the westerly flow of the Central Tasman water mass ceases in October–November, this South-west Tasman water mass, now occupying the central region of Bass Strait, flows east probably in association with an increase in the easterly flow of the North Bass Strait water mass along the western Victorian coast, as far as longitude 155° E. where it curves south and west (Fig. 18). An effect of this water mass has been detected in November–January at subsurface levels along the southern New South Wales

coast (Section V(*c*)(v)) and in the surface layers at latitudes well south of Hobart in early winter (Section V(*a*)(ii)).

From its chlorinity-temperature properties the East Tasmanian water mass could be formed by freshwater dilution of the South-west Tasman water mass. Its total phosphorus (Fig. 20) and nitrate content (Fig. 26) are consistent with such a genesis. The evidence of the Bass Strait surface samplings in 1954 (Fig. 21) showed that a water mass of similar properties occupied the north-east corner of the Tasmanian coast for the greater part of the year, although no 1954 summer data are

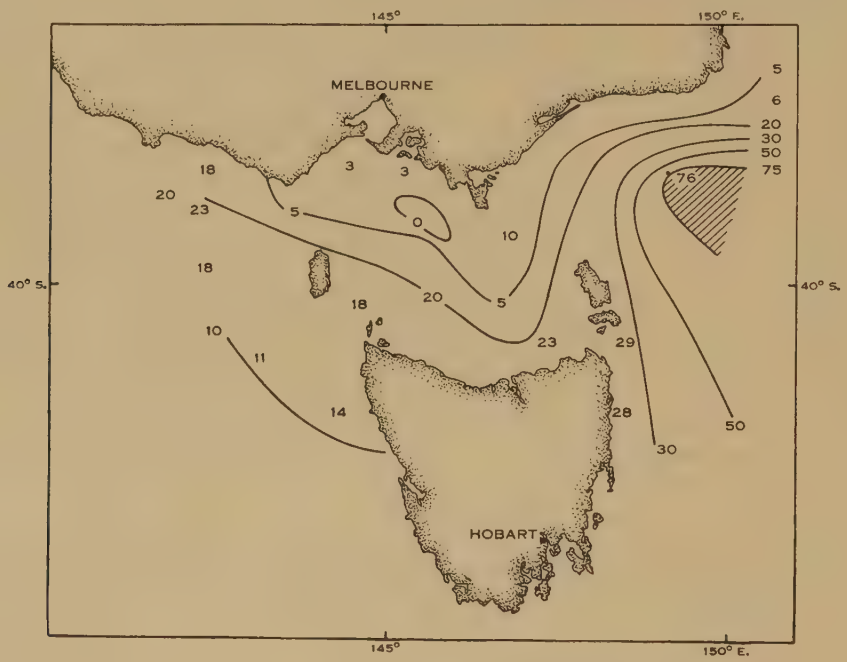

Fig. 26.—Mean concentration (μg nitrate N/l.) of nitrate nitrogen in the upper 50 m of Bass Strait waters, November 1954.

available. The maximum freshwater discharge into coastal waters in Tasmania occurs in the winter and spring, so that it is probable that the East Tasmanian water mass is formed by a dilution of the South-west Tasman water mass as it flows west through Bass Strait in the winter and spring. This water mass then persists in the north-eastern region of Tasmania until early summer, when it appears to move south along the east Tasmanian coast possibly in conjunction with a general reversal of flow through Bass Strait (Fig. 18).

The seasonal movements of the Sub-Antarctic water mass can only be followed at several positions in the southern Tasman Sea. Off the New Zealand coast, Schott (1935) located the subtropical convergence at a mid-point on the west coast of the North Island, during the winter months. According to evidence in Figure 6, this convergence does not appear to move much farther north than Cook Strait. Data for midwinter suggest that Sub-Antarctic water extends through Cook Strait at this

time. Garner (1954), using surface temperature records, states that Sub-Antarctic waters are rarely found off the west coast of the South Island. Temperatures alone, however, cannot provide positive identification of this water mass.

In the south-western Tasman the February and December 1954 data have both located the Sub-Antarctic water mass at about the same position in longitude 155° E. and latitude about 43° S., which suggests that its seasonal limits of distribution do not vary greatly in this region.

In Section V(*c*)(ii) evidence was given to support the genesis of the North Bass Strait water mass in South Australian waters west of longitude 140° E. If the high-chlorinity water mass found in Bass Strait along the Victorian coastline in March (Fig. 17) and in November 1954 (Fig. 20) is continuous with this water mass, then an easterly movement of the latter would have to commence before that month.

If the evidence of Section VI is accepted for the time and place of formation of the East Central New Zealand water mass, then it would have to move through Cook Strait in early summer to fit in with its position along the west coast of the North Island of New Zealand during the summer period (Fig. 6). This flow may be aided by, if not actually caused by, the northerly movement at this time of the subtropical waters along the west coast of the North Island.

VIII. Discussion and Conclusions

Garner (1954) has shown from a study of thermograph records that in 1950 and 1952 seasonal changes in the structure of the East Australian current were most pronounced towards the end of April and in October. These periods coincide with the maximum development of the South Equatorial flow and of the arrival of the Coral Sea water mass off Sydney, demonstrated in this paper. He also shows a secondary warm mass east of the main subtropical mass of the East Australian current. A broad zonal distribution of the Coral Sea water mass such as occurred in 1953 (Fig. 12) would explain this phenomenon.

Off the eastern approaches of Bass Strait Garner (1954) in January 1951 found a cold "lower"-salinity water mass. Later evidence (January 1952) indicated a north-going current associated with this colder water. The circulation of the South-west Tasman water mass described in this paper agrees with this evidence.

Garner, from a study of surface temperature gradients, considers that the subtropical convergence rarely occurs off the west coast of the South Island of New Zealand. However, chlorinity-temperature data in Cook Strait (C.S.I.R.O. Aust. 1955, 1956*b*) have been interpreted in this paper as characteristic of Sub-Antarctic waters. It is probable therefore that these Sub-Antarctic waters must have been driven north of the convergence along the west coast, or must have entered Cook Strait from the east. The former mechanism has been accepted in the preparation of Figure 6, but it is very probable that the boundary between the Sub-Antarctic and Central Tasman water masses in this figure is not the subtropical convergence. Wood (1954) has characterized certain water masses in the Tasman and Coral Seas from a study of dinoflagellates. He identified a Coral Sea dinoflagellate population as well as a South Equatorial in the East Australian current.

The findings of this paper regarding the small extent of Sub-Antarctic influence on conditions around Tasmania also agree with his dinoflagellate evidence. Olsson (1955), from a study of tidal streams in the eastern approaches of Cook Strait, found residual currents to the north at the entrance and to the south in the central portion of the strait in May 1951. From his data it is impossible to decide whether any significant net transport through Cook Strait was occurring in this month. However, May would fall in the transition period between the westward flow of the East Central New Zealand in early summer and the eastward flow of the Sub-Antarctic water mass in winter, proposed in this paper. Because of this, transport of water through the strait would not be significant in this month.

The major conclusions of this paper are summarized in Table 2. Although these conclusions are based upon the minimum of evidence it is hoped that their use will enable future surveys of the region to be directed into regions and seasons of major importance in the study of the water-mass structure and circulation of the Tasman Sea.

IX. Acknowledgments

It is impossible to acknowledge adequately the work of the many persons who have contributed, over the years since 1939, to the collection of the oceanographical data of this paper.

However, the captains and crews of F.R.V. *Warreen* and *Derwent Hunter* should have special mention in view of the small and personally uncomfortable nature of their ships for oceanic survey work. The Huddart Parker Company and the officers of T.S.M.V. *Wanganella* and *Taroona* are especially thanked for their most generous assistance in the surface sampling of the Tasman Sea and Bass Strait. The officers of the R.A.N. survey ships *Warrego* and *Barcoo*, who collected valuable slope and shelf hydrological data in New South Wales waters, are also thanked.

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TROUT POPULATIONS AND HABITATS IN NEW SOUTH WALES

By J. S. Lake*

[*Manuscript received April* 15, 1957]

Summary

Surveys of most of the trout waters in New South Wales have been made. Relevant data of the trout areas are given in respect to geography, generalized topography, and climate. Chemical and physical conditions of the waters are tabulated. Growth rates of trout and quantitative data on the bottom fauna of some streams have been determined. It is shown that the biological, chemical, and physical characteristics of the trout habitats are related and interdependent to a marked and consistent degree. The waters are separated into three groups on the basis of trout growth. The data suggest that the majority of waters in New South Wales often provide conditions which are limiting for trout.

Preliminary population and mortality studies have been made on small sections of nine rivers and on one small lake. The results of a creel census are given. The information from these sources confirms conclusions obtained from the habitat surveys. In addition evidence is presented indicating that certain management procedures should be modified. These include legal length, closed season, and stocking of streams. It is suggested that some of these modifications would have the additional benefit of reducing predation, and that hatchery-reared trout could be utilized on a much wider basis than at the moment for cold-water fish farming.

I. Introduction

Brown trout (*Salmo trutta* L.) were introduced into New South Wales streams in 1888 and rainbow trout (*S. gairdneri* Richardson) in 1894.

As a result of these and subsequent introductions most waters on the tablelands, from Tenterfield in the New England district to the Victorian border, support stocks of either or both of these species of non-indigenous Salmonidae.

After persistent requests by anglers to improve trout fishing, the Fisheries Branch of the Chief Secretary's Department initiated research into the trout fisheries in 1949. The only other work carried out in New South Wales was that of McKeown (1934*a*, 1934*b*, 1936, 1937, 1955) on the food of trout. The purpose of the present work was to try to find ways of improving fishing and of using hatchery-reared trout most efficiently and economically.

The main objectives were to collect data on the trout waters and their watersheds. Considerable information had already been published on the geology, topography, climate, and other factors relating to the watersheds. It was considered that this information together with growth rate and bottom fauna data would give some indication of the trout production potential and the suitability of streams for trout. Another objective was to carry out population studies in as many places as possible. Unfortunately the time, facilities, and staff available precluded any detailed work, and it was only possible to make preliminary assessments of populations

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on small sections of a number of streams and on one lake. Nevertheless it is considered that this work is worthy of recording, particularly when viewed in the light of the habitat surveys. During the period 1949–1952 surveys were made of the majority of trout waters in the State. These surveys included collection of data on the geography, topography, geology, climate, timber, land use, and soil associations of watersheds; chemical and physical analyses of water, periodic bottom food sampling, flow, and type of stream beds; and weights of stomach contents, age, and growth rates of the fish.

It soon became evident that there were wide variations in ecological conditions, but that most of the trout waters could be placed into one of three distinct groups, each group having certain distinguishing characteristics within a limited range.

Since the latter part of 1951 up till the end of 1955 additional studies have been made on small sections of a number of streams, and on a lake. These studies have included work on populations, bottom fauna, and artificial enrichment of a lake with inorganic fertilizers. During this work readings and tests were still made on as many streams as possible so that a good cross section of results under all conditions would be obtained.

For the purpose of publication much of the detail concerning individual streams has been omitted, but it is available for viewing at the Fisheries Branch of the Chief Secretary's Department.

II. Material and Methods

(*a*) *Geography, Topography, Geology, Climate, Timber, Land Use, and Soil Associations*

Information relating to the watershed and climate was obtained from the reports and regional maps of the New South Wales Premier's Department on the following: Clarence River Region (1945), Upper Murray Region (1947), Lachlan Region (1949*a*), Monaro–South Coast Region (1949*b*), Murrumbidgee Region (1949*c*), Southern Tablelands Region (1949*d*), Namoi Region (1950), New England Region (1951), Oxley Region (1956), Mitchell Region (unpublished data), and Sydney Region (unpublished data).

The streams were placed in water systems for this purpose and only a broad outline of some of the different factors are given. Full details with maps are available in the abovementioned publications. Figure 1 shows a diagrammatic map of the location of the main trout waters and major towns.

(*b*) *Physical and Chemical Surveys*

Most analyses were made under field conditions immediately after samples were taken. The tests were restricted to surface water temperature, pH, total alkalinity, and total dissolved solids. Only in a few special instances was dissolved oxygen determined. It was considered that most streams were well aerated, with oxygen near saturation. All these tests were carried out for a period of 6 years at irregular intervals, but nearly always over at least three periods each year. During these periods the tests were made at several stations in each stream and where possible at distances no greater than 10 miles apart. These tests have thus

been made at various times of the day, under varying conditions, and in all seasons for each stream.

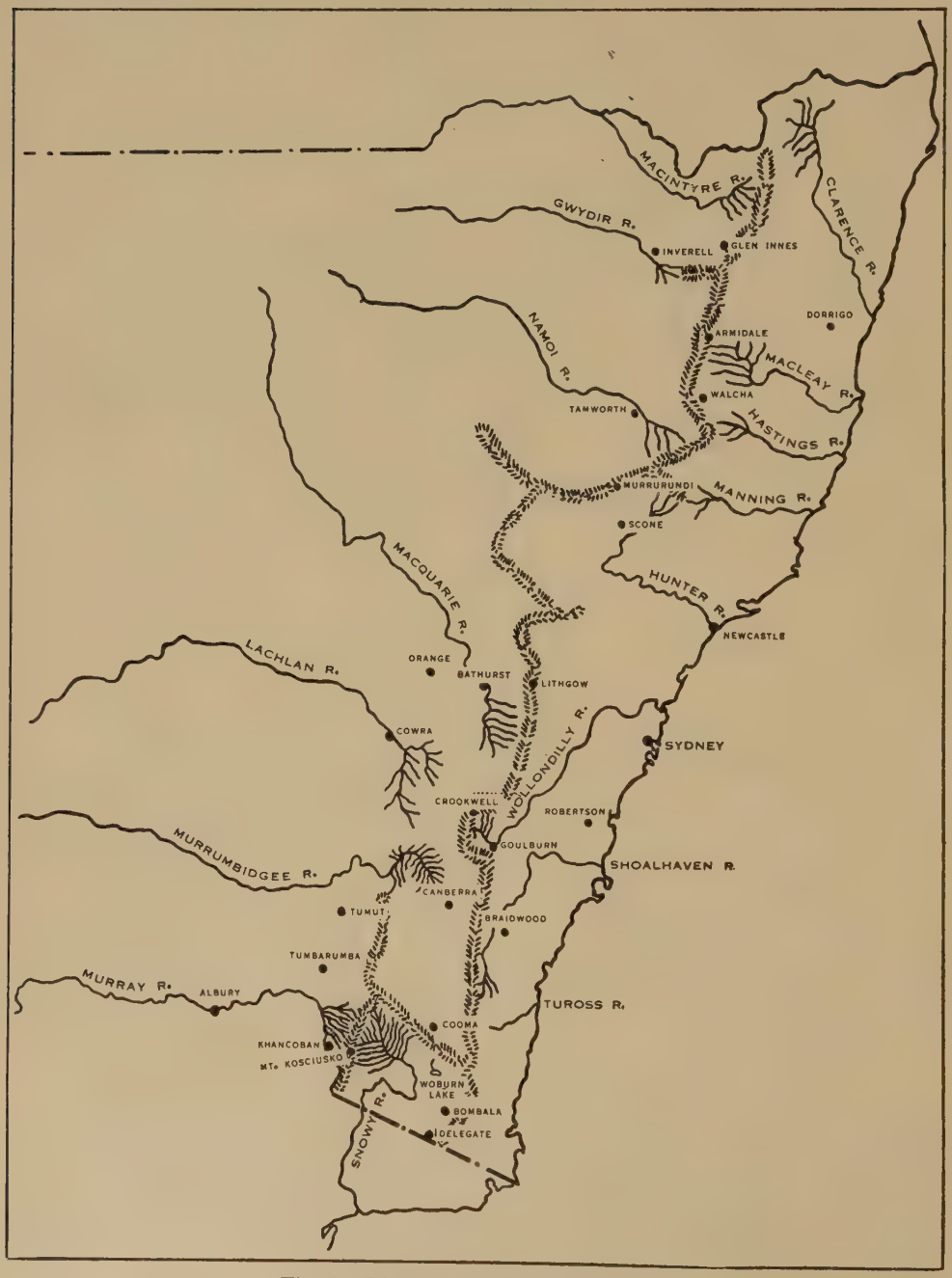

Fig. 1.—River systems and main towns.

(i) *Hydrogen Ion Concentration.*—pH was measured with a Lovibond comparator using glass standards. The indicator solutions used were bromocresol

purple for the 5·2–6·8 range, phenol red for the 6·8–8·4 range, and thymol blue for the 8·0–9·6 range.

(ii) *Total Alkalinity.*—This was determined by titrating 100-ml samples with N/50 hydrochloric acid using methyl orange as indicator, and was expressed as milligrams of calcium carbonate per litre.

(iii) *Total Dissolved Solids.*—These were estimated by filtering and then evaporating and drying at 180°C for 1 hr.

Samples were collected and brought back to the laboratory for this determination.

(iv) *Dissolved Oxygen.*—This was estimated by Winkler's method.

(c) *Bottom Food Sampling*

Bottom fauna was sampled during the chemical and physical surveys. Samples of 1 sq. ft were selected in at least five places at each station. Attempts were made to select representative areas of river bottom as determined by visual means. A square-foot sampler was used. This consisted of a reference frame 1 ft square, attached to this vertically being another frame 1 ft square to which was attached a cloth net.

In using the sampler, the stones lying within the reference frame were picked up and washed in front of the mouth of the net. All animals from each sample were weighed after drying on blotting paper for 5 min. The average area a certain length of stream covered was roughly determined by "dividing" the stream up into rectangles every time there was a reasonable variation in width. Because this method was somewhat approximate, values for bottom fauna have been expressed to the nearest 10 lb/acre.

(d) *Age and Growth Rate of Fish*

Usually the ages and growth of the trout were determined from the scales. In a few cases it was possible to make checks on the accuracy of this method. These checks were possible when a water containing no trout was stocked for the first time, and again in nine instances when fin-clipped fish were liberated. Whenever fish were marked they were anaesthetized in a solution of 0·5 per cent. ethyl carbamate. This technique saved considerable time and minimized handling of the fish. Contrary to the opinion of some workers such as Allen (1951), all evidence suggested that scale reading was not too subjective and that the results obtained were reasonably reliable.

Marked fish were held in the hatchery for at least 2 weeks prior to liberation. No unusual mortality resulted.

Most scale samples were collected on a voluntary basis by anglers. Envelopes were issued and over 5200 samples were returned. Anglers supplied information on the envelopes relating to the length, weight, sex, species, and time and place of capture.

Scales were dry-mounted between glass slides, and a projection microscope used so that the scale image was projected down onto a table where an adjustable scale was used for reading off the lengths at each winter check.

(*e*) *Stomach Contents of Fish*

The food eaten by trout was obtained mainly by collectors who forwarded stomachs together with details of the fish captured. These samples were preserved in 8 per cent. formalin. The contents were weighed after draining on blotting paper for 2 min. McKeown (1934*a*, 1934*b*, 1936, 1937, 1955) and Butcher (1945, 1946) have given results of the species, and percentages of each, found in material examined by them from New South Wales and Victoria respectively. The composition of the present material was much the same. Pertinent results from this work are shown in Figure 2.

(*f*) *Condition Factor of Fish*

It was necessary to rely on information forwarded by anglers, and all weights and lengths were expressed in pounds and inches respectively. The condition factor used, calculated according to Corbett's method, is:

$$\frac{(\text{Weight in pounds}) \times 10^5}{(\text{Length in inches})^3}.$$

For trout a condition factor of 40 is considered satisfactory.

(*g*) *Populations and Mortalities of Trout*

Except for the small lake of surface area 25 acres, available facilities made it possible to carry out population checks only on small sections of the streams selected. A 4 acre area or in a few cases a 3 acre area was considered suitable under the circumstances. The width of the stream then determined the length to be studied, which varied from $\frac{1}{2}$ mile to 3 miles. Within each stream all acre sections were similar in most respects.

Marked fish showed that there was little migration, and thus the small areas should not have produced any great errors. Surber (1937) and Shetter and Leonard (1942) conducted population studies on small areas of a Virginian and a Michigan trout stream respectively. Their work showed that studies of small areas can yield useful results.

Several methods were used for determining populations. Methods (i) and (ii) were most frequently employed. These are based on the short-period simultaneous marking and recovery estimation of populations.

Method (i).—Two nets were placed across the river in convenient situations so that about 1 acre of stream was enclosed by the nets. A third net was then moved up from the down-stream net to the other one. This was repeated until at least 30 fish were caught or eight nettings had been made. Captured fish were measured, weighed, and sexed, a few scale samples taken, and one pelvic fin removed. Several hours later, or on the following day, the third net was again moved up between the two fixed nets. On some occasions this procedure had to be repeated in order to obtain sufficient returns.

Statistical tests of significance showed that sufficient returns were made when about 30 per cent. of the fish captured were marked. This was accomplished in most

cases except for Lake Canobolas. It can therefore be assumed that the population for Lake Canobolas has probably been underestimated, because $\chi^2 = 12{\cdot}3$, and for three degrees of freedom, the probability was less than 1 per cent. Even in the case of the Upper Snowy River, which showed a smaller percentage of marked fish captured than any of the other rivers, $\chi^2 = 4{\cdot}408$, and for four degrees of freedom the probability was about 35 per cent. There is therefore no reason to doubt that the efficiency of netting was satisfactory, and indeed excellent in all cases other than Lake Canobolas. The lower efficiency for the upper Snowy River was probably due to the fact that such large lengths of stream had to be netted. The sections of the upper Snowy River netted were much less rugged than that illustrated (Plate 2), and in fact were easier to net than the other streams, notwithstanding the greater length, because of the stable and square nature of the banks.

The total population for the small sections was calculated from Schnabel's (1938) formula

$$P = \frac{M(t)\,C(t)}{R(t)},$$

and the progressive average populations of the 2, 3, and 4 acre portions were calculated from the formula

$$P = \frac{\Sigma M(t) C(t)}{\Sigma R(t)},$$

where P is the population, $M(t)$ the number of marked fish at large at the end of the nettings, $C(t)$ the number of fish captured, $R(t)$ the number of marked fish recaptured, and (t) the netting date. Rounsefell and Everhart (1953) give details of this technique.

During subsequent netting periods a different 1 acre section was selected until population in all 4 acres had been estimated. Consequently populations were determined in each acre section at different times of the year and often under greatly varying conditions.

The population could be calculated for each year class and thus the percentages of different age groups could be determined for all fish captured at each netting.

Method (ii).—In streams with large pools and in the lake where flow was not a problem gill nets were used. The fish caught in the first netting were marked and at least a full day was then given for the marked fish to become distributed evenly amongst the unmarked ones.

Different-sized meshes were used so as to reduce the possibility of selective fishing for a particular size or year class.

The above two methods only allowed the capture of fish from 8 or 9 in. upwards. Lights were occasionally used at night for rough observation of smaller fish, but no data are presented in connexion with these. The direct estimation of fry is extremely difficult. The Brown Trout Research Committee (Yonge 1952) showed that, when disturbed, fry can burrow into suitable stream beds and reach depths beyond the reach of most predators in a very short time.

In Lake Canobolas, where nettings were carried out in scattered areas, the lake was considered as one unit, and fish marked on previous netting dates had to be considered in the calculations. This was also the case in one acre section of the upper Snowy River. It was also necessary to take into consideration the capture of marked fish. For example, for Lake Canobolas (Table 6), the marked fish at the end of the netting in November 1954 is the sum of the fish marked in October 1954, plus additional fish marked, minus those captured by anglers. The capture of marked fish was recorded for Lake Canobolas and nettings were conducted over a relatively short period, except for the last netting. Natural mortalities between the shorter netting periods were neglected.

In Table 6 the percentages of the different age groups are those resulting from all nettings. The fact that fish increased in age from one netting to another does not matter if the population is in equilibrium, since although some 1+ fish became 2+ and 2+ became 3+, at the same time some 0+, not previously recorded, were taking the place of the 1+ fish which became older.

Results of the population studies are summarized in Table 6. The recorded mean weight of fish caught is the mean of all fish captured at each netting. This mean weight should be fairly constant, for the reason given above in connexion with the percentages of different age groups. Unless the stream was grossly understocked it would obviously be impossible for the mean weight to go on increasing. The fish were marked and weighed after anaesthetizing in a solution of ethyl carbamate. Weighing was carried out after allowing a few seconds for excess water to drip from the fish.

Method (iii).—The estimation of the egg population was based to a large extent on the fecundity of the mature female population (Brown and Kamp 1942). Other methods such as numbers of redds, and efficiency of fertilization and hatching have been used to estimate both egg and fry populations (Hobbs 1940, 1948; Affleck 1952*b*; Briggs 1953). Egg counts made on over 100 fish from different rivers in New South Wales showed that fish from 1 to 5 lb had progressively larger numbers of eggs but fish larger than 5 lb did not show any appreciable increase in egg number. On the average 900–1050 eggs were found per pound weight of fish, depending on the stream. This result is no doubt very approximate owing to the small number of samples of fish of varying weight taken from different streams. Allen (1951) states that the relation between number of eggs and weight of fish is curvilinear; nevertheless for the purpose of egg estimation 1000 eggs per pound weight of fish was used because the results, as used, are only of a general and relative nature.

Method (iv).—In a few instances rotenone was used in pools during dry weather conditions when flow was at a minimum. This method eliminated any selective fishing, but since all the fish were killed it naturally had its disadvantages. This method can be useful for testing the accuracy of results obtained by other methods. Krumholz (1944) tested other methods, using rotenone, in Michigan. The rotenone was finely ground and mixed with water to form a paste, prior to distributing in the stream.

Rainbow and brown trout have not been separated in the results. Rainbow trout is the most prevalent species although brown trout are becoming more numerous in several localities.

TABLE 1

TROUT WATERSHEDS OF NEW SOUTH WALES

River System	No. of Streams	Altitude		Gradient*		Annual Rainfall		Seasonal Droughts†		Mean Air Temp.‡	
		Max. (ft)	Min. (ft)	Max. Slope	Min. Slope	Mean Max. (in.)	Mean Min. (in.)	Length (months)	Period of Year	Hottest Month (°C)	Coldest Month (°C)
EASTERN WATERSHED											
Clarence River	8	5000	2000	>15°	> 8°	60	35	0–4	W–S	22	1
Macleay River	9	5000	2000	>15°	> 3°	60	20	0–4	W–S	20	1
Hastings River	4	3500	3000	<15°	> 8°	>60	>60	0	—	22	1
Manning River	3	5000	4000	>15°	< 3°	60	25	0	—	>22	7
Hunter River	2	5000	1500	>15°	< 3°	40	20	0–4	W–S	>22	7
Wollondilly River	4	4000	2500	>15°	> 3°	<40	<35	0–4	W–S	20	1
Shoalhaven River	8	3000	2000	<15°	< 3°	60	25	0	—	20	1
Tuross River	1	3000	2500	>15°	15°	35	20	2–4	W–S	20	1
Snowy River	20	7000	3000	>15°	< 3°	100	15	1§	S–A§	<12§	< 0
								8–10	W–S	20	
Woburn Lake	1	3000	3000	< 8°	> 3°	>15		8–12	W–S	20	1
WESTERN WATERSHED											
McIntyre River	6	4000	2500	<15°	< 3°	40	20	0–4	W–S	22	1
Gwydir River	4	4500	3000	3°	< 3°	40	20	0–4	W–S	22	1
Namoi River	6	3500	2000	< 8°	> 3°	40	25	0	—	20	1
Macquarie River	8	4000	2500	8°	> 3°	<40	<35	1–4	S–A	22	1
Lachlan River	13	3500	2000	>15°	< 8°	>35	<35	0–4	S–A	22	1
Murrumbidgee River	24	5500	2000	>15°	3°	60	15	4–8‖	W–S‖	20	1
							(usually >35)	1	S–A		
Murray River	11	6000	1000	>15°	> 3°	>60	<35	1–4	S–A	20	< 0

*Gradient sometimes differs markedly for different streams and even within a stream on the same watershed.

†Seasonal drought period is that in which the monthly rainfall is less than 2 in. Some parts of some watersheds have no seasonal droughts. W–S, winter–spring; S–A, summer–autumn.

‡These mean air temperatures are for the hottest and coldest zones on the watershed. The mean air temperature for the hottest month never drops much below 12°C.

§Upper reaches of Snowy River.

‖Upper reaches of Murrumbidgee River.

TABLE 2

TROUT STREAMS OF NEW SOUTH WALES

River System	Group 1	Group 2	Group 3
Clarence R. (E)*	Nymboida R.	Guy Fawkes R. Beilsdown R. Main Water	Jock's Water Major's Ck. Allan's Water Coutt's Water
Macleay R. (E)	Rockvale Ck. Boundary Ck. Styx R.	McLeod's Ck. Tia R. Apsley R. Oakey Ck.	Serpentine R. Barwick Ck.
Hastings R. (E)		Ellenborough R.	Belford's Ck. Norrie's Ck. Allan's Ck.
Manning R. (E)			Barrington R. Gloucester R. Gummi Ck.
Hunter R. (E)	Page's R.	Upper Hunter R.	
Wollondilly R. (E)	Marrangaroo Ck. Ginkin Ck.	Tuglow R.	Kowmung R.
Shoalhaven R. (E)	Upper Shoalhaven R.	Mongarlowe R. Jerrabattgulla Ck. Mt. Elrington Ck. Thurralilli R. Verneilly R. Yarrunga Ck. Wallungundi R.	
Tuross R. (E)		Upper Tuross R.	
Woburn Lake (E)	Woburn Lake		
Snowy R. (E)	Mt. Cooper Ck. Cambalong Ck. MacLaughlin R. Bobundara Ck. Spencer's Ck. Rendezvous Ck.	Wallendibby Ck. Crewah R. Lower Snowy R. Three Mile Dam Bombala R. Coolumbooka R. Delegate R. Moonbah R.	Upper Snowy R. Gungarlin R. Upper Eucumbene R. Thredbo R. Burrengobuggy R. Lower Eucumbene R.
McIntyre R. (W)	Beardy R. Furracabad Ck. Wellingrove Ck. Deepwater R. Paradise Ck. Upper McIntyre R.		

TABLE 2 (*Continued*)

River System	Group 1	Group 2	Group 3
Gwydir R. (W)	Sandy Ck. Ollera Ck. Moredun Ck. Boorolong Ck.		
Namoi R. (W)	MacDonald R. Ingalba Ck. Cobrabald Ck. St. Leonard's Ck. Warrah Ck.	Dungowan Ck.	
Macquarie R. (W)	Campbell's R.	Fish R. Fish River Ck. Duckmaloi R. Sodwalls Ck. Lake Canobolas Upper Bell R. Molong Ck.	
Lachlan R. (W)	Abercrombie R. Belubula R. Mandurama Ck. Gallymont Ck. Coombing Rivulet Lachlan R. (Wyangala) Burra Ck. Crookwell R. Wheeo Ck. Lost R. Grabben Gullen Ck.		Little R. Isabella R.
Murrumbidgee R. (W)	Queanbeyan R. Molonglo R. Goodradigbee R. (Wee Jasper) Adjenbilly Ck. Cooma Ck. Kydra R. Kybean R. Pepper's Ck. Badja R. Rock Flat Ck.	Cotter R. Upper Tumut R. Lower Tumut R. Adelong Ck. Upper Murrumbidgee R. Lower Murrumbidgee R. Lower Gilmore Ck. Goobraganda R. Yarrangobilly R. Umaralla R. Clear Ck.	Upp. Goodradigbee R. Upper Gilmore Ck. Brownley's Ck.
Murray R. (W)	Murray R. (Hume Weir) Mannus Ck. Bell's Ck.	Swampy Plains R. Geehi R. Indi R. Valentine R. Tumbarumba Ck. Paddy's River Dam	Paddy's R.

*E, eastern watershed; W, western watershed.

(*h*) *Creel Census Data*

During the 1954–55 trout season a creel census was made. This was conducted by issuing a special licence on the back of which anglers were requested to supply certain details relating to their catch and to return the information at the end of the season.

The number of returns was disappointing but the results do show some interesting points. Unfortunately these results cannot be related to the work on populations. This creel census is now being made annually.

III. Results

(*a*) *Surveys of Habitats*

The trout waters of New South Wales are, in the main, restricted to the tablelands. In this area both the eastern coastal rivers and westward-flowing rivers find their source. Most of the upper tributaries of these rivers are trout streams. Ten of these rivers or water systems which carry trout are on the eastern watershed. Seven are on the western watershed, all of which eventually join with the Murray River.

A major difference between these rivers is that those on the eastern watershed are inhabited by eels and those on the western watershed are not.

Table 1 shows these water systems and the number of main trout streams flowing into them; the latter total 132. This number is somewhat arbitrary since minor tributaries which are not very important are left out. The combined mileage of the streams is estimated at about 10,000 miles. Only mean, or maximum and minimum, results for altitude, gradient, rainfall, and air temperature are given in this table since full details are available in the publications (listed previously) of the New South Wales Premier's Department. Specific detailed data for each stream have been collated and are available at the Fisheries Branch.

The streams are listed in Table 2 under their watersheds and have been placed into one of three groups according to trout growth. Those streams in group 1, which constitute 42 per cent. of the total, produced trout of fast growth. About 38 per cent. of the streams are in group 2. These streams produced trout of slower growth. The remaining 20 per cent. of the streams produced trout of slow growth. These have been placed in group 3.

There were instances where a stream had headwater regions which fitted into group 3, and yet the main portion of the stream fitted into groups 1 or 2. Frost (1945) also showed the variation in growth of trout in acid and alkaline waters in different parts of the one stream.

Many chemical, physical, and biological characteristics also fell within a particular range for each group. The mean results for all streams in each group are shown in Table 3.

Only maximum temperatures recorded are shown because it is these which are so important in connexion with survival of trout in streams in New South Wales. Daily temperatures for a whole year are only available for the Snowy River at Jindabyne. These were collected in 1945 and 1946 by Mr. R. Payten, who kindly supplied the details. The highest temperature from September 1945 to August 1946

was 29°C, taken in mid January. The lowest temperature was 1°C, taken towards the end of June. The maximum daily fluctuation of 7·4°C was recorded at the end of February. The average daily fluctuation was 3·1°C.

Fish from some streams were infected with a larval nematode, *Eustrongylides phalacrocoracis* Johnston & Mawson.

Some additional notes are necessary in regard to the lake habitat, which was improved by the addition of inorganic fertilizers.

Lake Canobolas is an artificial lake formed by a concrete wall across Molong Creek about 5 miles down-stream from its source. Molong Creek rises on Mount Canobolas at an altitude of a little over 4000 ft. From its source to the lake this creek

TABLE 3

CHEMICAL, PHYSICAL, AND BIOLOGICAL CHARACTERISTICS OF THE TROUT WATERS

Characteristic	Mean No. of Readings per Stream	Group 1	Group 2	Group 3
No. of streams		55	50	25
Per cent. of total streams		42	38	20
Mean pH	17	8·0	7·2	6·9
Mean total dissolved solids (p.p.m.)	5	450	170	83
Mean total alkalinity (mg/l. as $CaCO_3$)	17	92	30	20
Mean max. and range of water temp. recorded (°C)		26·2 21·5–28·5	24·7 21·1–28·8	21·7 17·6–26·1
Mean bottom fauna (lb/ac) Determined for x streams	100	570 $x = 15$	250 $x = 11$	90 $x = 3$

averages about 5 ft in width. Most pools are 2 to 3 ft deep, some a little deeper. The flow is moderate to fast and there are some good gravel sections in the upper reaches. Sudden heavy downpours often occur and bring down considerable quantities of silt. However, erosion is being checked on this watershed, which is used for orchards and to a small extent for pig raising. During normal flow the stream is typically 3–4°C warmer where it enters the lake than at its source.

The lake covers an area of 25 acres and is 25 ft deep towards the overflow or bottom end. Much of the lake is very shallow, having a depth of 2–15 ft. The area around the lake is well grassed and sparsely populated with trees. During the summer months the lake becomes thermally stratified with the thermocline at relatively shallow depths, usually between 8 and 14 ft. Complete oxygen depletion did not occur in the hypolimnion when readings were taken in December 1954, although it was reduced sufficiently to be uninhabitable for trout. The lake is

edaphically oligotrophic. Trout preferred the temperature range of 13–15°C in the thermocline to that of the epilimnion, where temperatures were as high as 22°C. This was borne out when netting was carried out at different depths during population studies. Most trout were gilled in the nets between 8 and 11 ft depth.

During 1953 and 1954 four applications of inorganic fertilizers were made to the lake. On the first occasion finely powdered limestone was added at the rate of 30 lb/ac. On subsequent applications finely ground limestone (5 lb/ac), superphosphate with 22 per cent. available phosphoric acid (18 lb/ac), ammonium sulphate with 21 per cent. available nitrogen (19 lb/ac), and muriate of potash with 60 per cent. available potassium oxide (6 lb/ac), were added. The second application was scattered over the shallow portions of the lake (that area where the depth was less than 6 ft). The other applications were added to the stream just before it enters the lake. In each case the stream was running fast and mixing was very good. The fertilizer could be seen entering the lake at one side, from where it travelled almost around the whole lake before dilution made it impossible to trace further.

This artificial enrichment appeared to have several effects. The water in the lake cleared much more quickly after storms and indeed has remained fairly free of suspended silt up to the present. This is partially due to improved watershed conditions as mentioned earlier. Prior to fertilization small areas of rooted aquatic plants, mainly *Myriophyllum*, *Elodea*, and *Potamogeton* spp., occurred near the edges and shallows to a depth of 2 ft. These aquatic plants increased considerably after fertilization, particularly the *Elodea* spp., which are now present in the lake to a depth of 10 ft. The plant growth does not interfere with fishing to any great extent.

No accurate quantitative measurements were made of plankton. Few freshwater shrimps (*Paratya* spp.) were previously found, but following fertilization a small hand net when scooped through the water, particularly when near the aquatic plants, was found to be full of these crustaceans. Almost without exception the stomachs of trout contain large quantities of these shrimps, now typically 60 per cent. of the food eaten. Prior to fertilization less than 2 per cent. of the diet consisted of shrimps. Trout from the lake are now more brilliantly coloured, the flesh is orange, and the ova are a deep pinkish orange, no doubt due to a larger intake of the carotenoid astaxanthin which occurs in shrimps (Grangaud 1952).

The length and weight of the trout at all ages increased. Prior to fertilization 128 fish samples gave scale readings of l_1 5·2, l_2 11·5, l_3 14·1, and l_4 16·0. The condition factor averaged 38. After fertilization 476 fish samples gave scale readings of l_1 7·6, l_2 13·2, l_3 15·2, and l_4 16·8. The condition factor averaged 48. The percentage mean increments in length actually decreased, but nevertheless the percentage mean increments in weight were greater following fertilization. This decrease in growth rate but increase in size for age was due to the greater length attained during the first year, the improvement in condition of the fish, and the fact that 3- and 4-year-old fish caught in the 2 years following fertilization showed pre-fertilization growth for their first, and sometimes second, years. This last factor has caused the l_1 and l_2 for post-fertilization to be smaller than they should be. The difference would only be slight, however, as the majority of fish taken were only in their third year or younger.

It appears that an increase in pH value, alkalinity, total dissolved solids, and bottom fauna resulted. It is not possible to be definite as to what extent the fertilization caused these increases because of the small number of readings taken prior to fertilization at various seasons. In addition, most chemical tests made after fertilization were made within a week of the applications.

TABLE 4

GROWTH, CONDITION, SEX RATIO, SPECIES RATIO, AND OTHER CHARACTERISTICS OF TROUT CAUGHT

Characteristic	Group 1 (52 streams)	Group 2 (45 streams)	Group 3 (23 streams)
No. of trout	1808	2799	664
Mean L_1 (in.)*	8·4 (52)	6·7 (45)	4·9 (23)
Mean L_2 (in.)	16·2 (50)	12·8 (45)	9·6 (23)
Mean L_3 (in.)	20·1 (27)	16·6 (40)	13·6 (19)
Mean L_4 (in.)	23·8 (7)	19·4 (19)	16·3 (9)
Mean L_5 (in.)	25·8 (3)	22·5 (7)	20·0 (3)
Mean L_6 (in.)	28·0 (1)	26·3 (2)	
Mean L_7 (in.)		27·5 (1)	
Mean condition factor	47	42	39
Mean No. of males (%)	37	38	43
Mean No. of females (%)	63	62	57
Mean percentage of rainbow trout	81	51	88
Mean percentage of brown trout	19	49	12
Mean percentage of streams carrying rainbow trout only	67	33	80
Mean percentage of streams carrying brown trout only	12	16	4
Mean percentage of streams carrying both rainbow and brown trout	21	51	16
Mean age of trout caught (yr)	2·3	2·7	3·0
Mean wt. of trout caught (lb)	2·7	1·8	0·9
Mean length of trout caught (in.)	17·7	15·7	13·0

*Figures in parentheses are the number of streams from which samples were taken.

The main predator in this water is the large black cormorant, *Phalacrocorax carbo* L. An attempt is being made to eradicate these birds by shooting, and this should be of value in this particular case as spawning redds are often destroyed in Molong Creek by short sudden floods, resulting in possible under-population. Stocking of the lake is supplemented at the moment with hatchery-raised fish. Smith (1952, 1955) gives full details of improvements attained by fertilization and predator control on a lake.

TABLE 5

LIBERATION AND RECOVERY OF MARKED FISH

Water Stocked	Hatching Date	Liberation Date	Species	No. Stocked	Mean Length (in.)	No. Recaptured	Date of Recapture	Length (in.)	Age (yr)	Scale Reading	
										L_1 (in.)	L_2 (in.)
Woburn Lake*	—.x.50	—.xi.50	Rainbow	4000	1	35+	5.xii.51	15¾	1+	9	
							13.xii.52	23½	2+	9½	22
							23.xii.52	21¼	2+	9½	20¼
							5.xii.52	19¾	2+	6	18½
Tumut R.	—.x.50	1.iv.51	Rainbow	3000	4	9	8.xi.51	7¼	1+	7	
							8.xi.51	7½	1+	6½	
							3.xi.52	13½	2+	5¾	13
							18.i.53	12½	2+	6	11¾
							—xii.51	7–9½	1+		
Campbell's R.	—.viii.53	—.iv.54	Brown	750	5½	3	—.ii.55	14¾	1+	10¼	
							—.ii.55	13½	1+	7¾	
							15.i.56	21½	2+	9½	18¾
Tarlo R.	—.x.53	—.iv.54	Rainbow	2000	3½	3	—.x.55	No data given			
Belubula R.	—.x.53	—.iv.54	Rainbow	2000	3½	1	—.iii.55	No data given			
Jock's Water	—.viii.53	—.ii.54	Rainbow	3000	3	4	28.x.54	7¼	1+	5¾	
							28.x.54	9	1+	7	
							28.x.54	9½	1+	6¾	
							14.x.55	11½	2+	6½	10½

TABLE 5 (*Continued*)

Water Stocked	Hatching Date	Liberation Date	Species	No. Stocked	Mean Length (in.)	No. Recaptured	Date of Recapture	Length (in.)	Age (yr)	Scale Reading	
										L_1 (in.)	L_2 (in.)
Furracabad Ck.	—.viii.53	—.ii.54	Rainbow	3000	3	0					
Beardy R.	—.viii.53	—.ii.54	Rainbow	3000	3	0					
Delegate R.	—.ix.53	—.iii.54	Brown	3000	2½	0					
Lower Snowy R.	—.ix.53	—.iii.54	Brown	3000	2½	2	—.xii.55	14	2+	7½	12½
							—.ii.56	14½	2+	6	11½

*This lake contained no fish. It was previously dry and was filled by heavy rain; no stream flowed into it. It is known that many fish were caught from this lake and were not recorded. Two-year-old fish had fully matured gonads, and in November 1953, some died spawn-bound. These fish were then 3+ years old and weighed up to 9 lb.

(b) *Growth Rate of Trout*

Table 4 shows mean results for each group of streams for growth, condition, and other factors relating to the trout. Growth data are based primarily on scale readings. A total of 5271 scale samples were examined.

During examination of many scales from fish whose ages were known, a "winter band" formation was often laid down on the scales during the first summer. This would cause the age of a fish at subsequent periods to be read as 1 year older than it actually was.

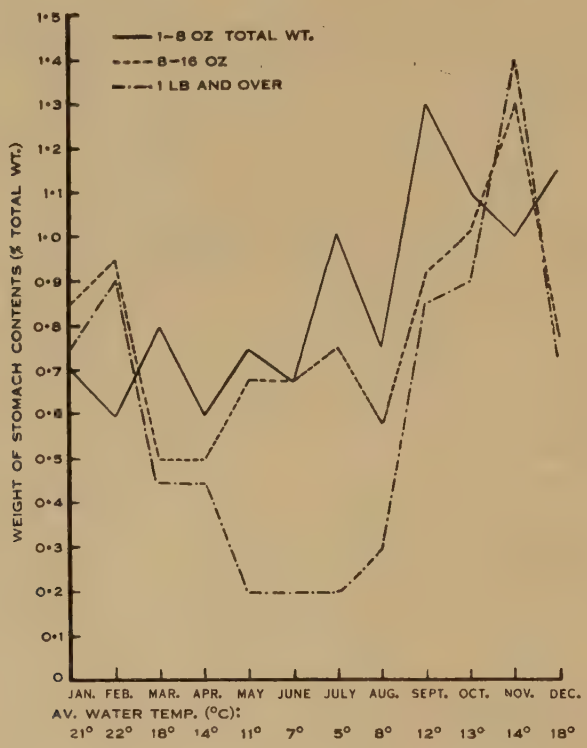

Fig. 2.—Weight of stomach contents as percentage of total weight of trout, Swampy Plains River, 1951.

Some unpublished results of scale reading by interested anglers were examined and it was obvious that many of the readings incorporated this error. Allen (1951) experienced this phenomenon in New Zealand also.

The liberation and recovery of marked fish substantiated the scale reading results.

Details of the waters stocked with marked fish and the returns are shown in Table 5. It is very likely that many more marked fish were caught and never recorded by anglers, even though notices near the streams and in the appropriate districts were displayed. Appeals were also made to anglers in the press and on their licences.

The results for rainbow and brown trout have not been separated. Examination of the growth of samples of the two species in a number of streams indicated that their growths do not differ markedly. In some streams growth is a little better for brown trout, usually in the first year. The opposite, however, also occurs. The brown trout caught by anglers are often larger than the rainbow trout but they are also older. Brown trout are apparently not so readily caught.

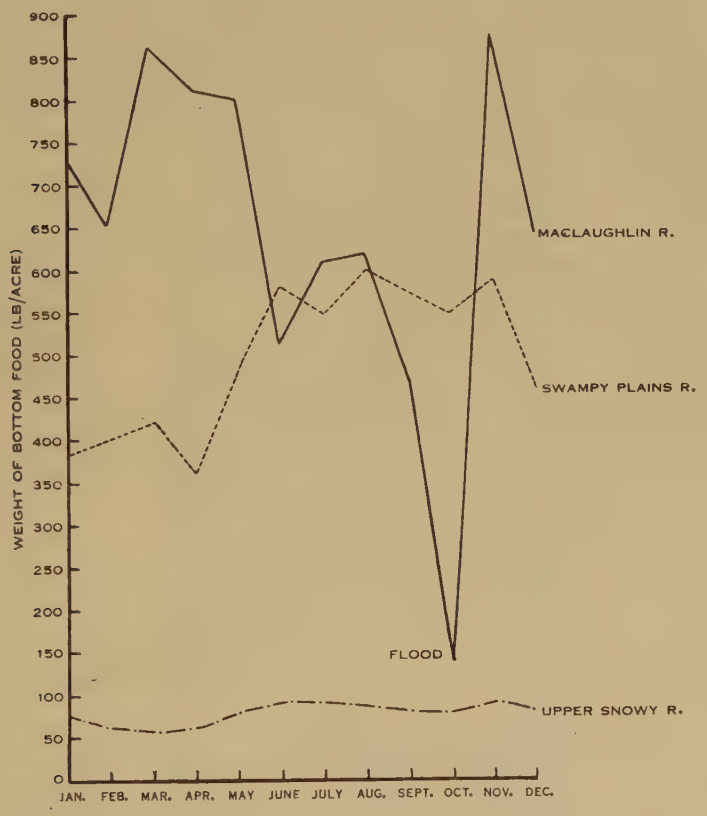

Fig. 3.—Weight per acre of bottom food in three streams during 1951.

(c) *Food of Trout and Bottom Fauna*

The amount of food found in the stomachs of trout generally gives no indication of good or poor growth conditions. Temperatures, and therefore rate of feeding and digestion, seem to be the more important factors in this regard (Purkett 1951). This is borne out by the fact that the weight of stomach contents, expressed as a percentage of the total weight of the trout, differed during the winter and summer months, particularly for mature spawning fish. Figure 2 shows these results for trout taken from the Swampy Plains River.

For trout up to 8 oz there was some variation and the average lay around 1 per cent. There is a strong indication that the stomach contents rose with rising temperatures during the spring to values between 50 and 100 per cent. higher than the

winter values, falling again as the higher summer temperatures were reached. For larger trout the differences were greater and for mature fish the spring values were about seven times greater than the winter values. This low winter ratio of stomach contents to total weight of mature fish may be partly due to increase in gonad size. Nevertheless it does point to quiescence of the fish during extremes of temperatures.

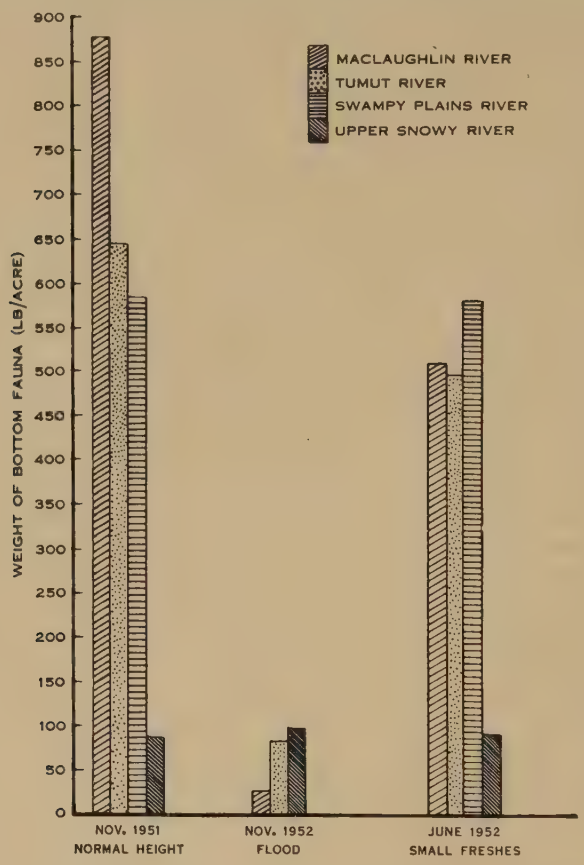

Fig. 4.—Weight of bottom fauna per acre in various types of streams under different conditions.

On the other hand the amount of bottom fauna gave some indication of good and poor growth waters (Table 3). It was necessary, however, to take many samples because of the enormous variations, particularly in those waters where the stream bed was unstable. Figure 3 shows the amount of bottom fauna for three different types of streams over the course of a year.

The weight of food on the bottom of the stream did not show any marked seasonal fluctuations. Flood conditions were much more important in regulating the abundance of bottom fauna. After floods the bottom fauna made a dramatic recovery in the MacLaughlin River. The physical nature of the stream undoubtedly

determines the extent of the fluctuations of bottom fauna during floods. Figure 4 shows the effect of floods and small freshes on bottom fauna in several streams.

When considering any relationships between food and growth of trout there are factors other than temperature which have to be considered. For example, Lovelace and Podoliak (1952) showed that dissolved minerals as well as the food affect the trout directly. By the use of labelled calcium they were able to show that dissolved calcium in the water entered through the gills and was distributed to the muscle tissue and bones by the blood-stream.

During the winter of 1952 there were almost continuous floodings of many of the streams in the State. These floods were severe, particularly in streams flowing through relatively flat country and in those waters in group 1. The effect on the fish population, particularly the eggs, fry, and fingerlings, was undoubtedly disastrous although the population studies were not extensive enough to give very accurate and quantitative results. It was obvious that in many streams the bed was completely disturbed and rooted aquatic plants and spawning redds were eliminated. In the MacLaughlin River, for example, the reduction of bottom fauna in this unstable stream was very severe immediately after flood conditions.

The aquatic flora and fauna and other limnological details of the Gara River on the New England tableland give some indication of the conditions and types of organisms found in many New South Wales streams. O'Farrell (1949) conducted a short-term limnological study on this river.

(*d*) *Population and Mortality Studies*

The population studies were made on the MacLaughlin, Campbell's, and Abercrombie Rivers, Boorolong Creek, Beardy River, Lake Canobolas, the Tumut, Fish, and upper Snowy Rivers, and Jock's Water. The results of this work are shown in Table 6. Details of methods and tests of significance have been given in Section II(*g*).

Fish smaller than 9 in. in Lake Canobolas and Boorolong Creek, and less than 8 in. in all other streams, are not accounted for in the results because the methods used did not allow of accurate assessment of these fish. These fish, however, would not make a big difference to the total weight of fish per acre even though their numbers are relatively great.

In the case of Lake Canobolas the population determined for July 1955 was about three times larger than expected. To a lesser degree this also applied to the upper Snowy River for March 1954 and May 1955. The reason for this is that natural mortalities were not taken into account, and the marked fish at the end of the netting were actually much less than shown.

It is evident from the estimate of the number of eggs produced per acre that the mortalities are enormous during the fish's early life. Flood and drought conditions also reduce the population of fish. During high temperatures limiting conditions prevail and fish either abandon major areas of the unsuitable streams or are even killed. Dead fish have been collected in the MacLaughlin and lower Snowy Rivers, and several reports have been received of dead fish in other streams during high water-temperature conditions.

TABLE 6

POPULATIONS OF TROUT

Stream	Netting Date (t)	Section Netted*	Marked Fish at End of Netting ($M(t)$)	Fish Captured ($C(t)$)	Marked Fish Re-captured ($R(t)$)	$\frac{M(t).\,C(t)}{R(t)}$	$\frac{\Sigma M(t).\,C(t)}{\Sigma R(t)}$	Age Groups Captured	Mean No. of Fish per ac†	Mean Wt. of Fish Caught (lb)	Wt. of Fish per ac† (lb)	No. of Eggs Produced per ac (estimate)
GROUP 1												
MacLaughlin River	May 1952	A (1 ac)	38	22	8	104	104	0+, 16%	46	2·8	170	30,000
(*Snowy R. system*)	Dec. 1952‡	B (1 ac)	25	20	10	50	74	1+, 49%				
Area netted, 4 ac	Oct. 1953	C (1 ac)	18	11	7	28	61	2+, 30%				
Length of stream	May 1955§	C and D		2	0	2		3+, 4%				
sections, 0·75 mile	(rotenone)	(2 ac)						4+, 1%				
Campbell's River	Aug. 1954	A (1 ac)	18	10	4	45	45	0+, 10%	34	3·1	105	12,000
(*Macquarie R. system*)	Nov. 1954	B (1 ac)	26	12	8	39	41	1+, 77%				
Area netted, 4 ac	Dec. 1954	C (1 ac)	11	8	3	29	39	2+, 11%				
Length of stream	Mar. 1955	D (1 ac)	6	4	1	24	38	3+, 2%				
sections, 1 mile												
Abercrombie River	Apr. 1954	A (1 ac)	52	32	16	104	104	0+, 3%	96	1·8	173	60,000
(*Lachlan R. system*)	Aug. 1954	B (1 ac)	58	30	20	87	95	1+, 47%				
Area netted, 3 ac	Nov. 1954	C (1 ac)	42	35	15	98	95	2+, 41%				
Length of stream								3+, 6%				
sections, 0·5 mile								4+, 3%				
Boorolong Creek	Mar. 1954	A (1 ac)	22	14	11	28		1+, 86%	22	2	44	3,000
(*Gwydir R. system*)	Feb. 1955§	B (2 ac)		3		3		2+, 11%				
Area netted, 4 ac	(rotenone)							3+, 0%				
Length of stream	June 1955	C (1 ac)	10	6	4	15		4+, 3%				
sections, 0·5 mile												

TABLE 6 (*Continued*)

Stream	Netting Date (t)	Section Netted*	Marked Fish at End of Netting ($M(t)$)	Fish Captured ($C(t)$)	Marked Fish Re-captured ($R(t)$)	$\frac{M(t).\,C(t)}{R(t)}$	$\frac{\Sigma M(t).\,C(t)}{\Sigma R(t)}$	Age Groups Captured	Mean No. of Fish per ac†	Mean Wt. of Fish Caught (lb)	Wt. of Fish per ac† (lb)	No. of Eggs Produced per ac (estimate)
GROUP 1 (*Continued*)												
Beardy River	Mar. 1954	A (1 ac)	32	19	12	51		0+, 2%	45	1·9	86	13,000
(*McIntyre R. system*)	(rotenone)							1+, 75%				
Area netted, 3 ac	Feb. 1955§	B (1 ac)		0		0		2+, 16%				
Length of stream	June 1955	C (1 ac)	24	13	8	39		3+, 3%				
sections, 0·5 mile								4+, 4%				
GROUP 2												
Lake Canobolas	Aug. 1954		70	52	2	1,820	1,820	0+, 0%	64	1	64	25,000
(*Macquarie R. system*)	Oct. 1954		119	50	4	1,488	1,598	1+, 1%				
Area netted, 25 ac	Nov. 1954		115	11	0	1,265	1,809	2+, 79%				
	Dec. 1954		126	100	7	1,800	1,804	3+, 12%				
	July 1955‖		148	70	2	5,180		4+, 8%				
Tumut River	May 1952	A (1 ac)	52	40	19	110	110	0+, 0%	90	1·5	135	50,000
(*Murrumbidgee R. system*)	Dec. 1952‡	B (1 ac)	41	26	11	96	102	1+, 32%				
	Oct. 1953	C (1 ac)	26	20	7	74	99	2+, 42%				
Area netted, 4 ac	Mar. 1954	D (1 ac)	30	15	5	90	98	3+, 18%				
Length of stream	May 1955	A (1 ac)	18	9	2	81	97	4+, 6%				
sections, 0·5 mile								5+, 2%				
Fish River	Aug. 1954	A (1 ac)	62	60	38	98	98	0+, 0%	102	1·1	112	40,000
(*Macquarie R. system*)	Nov. 1954	B (1 ac)	40	26	9	115	101	1+, 22%				
Area netted, 4 ac	Dec. 1954	C (1 ac)	42	31	17	77	95	2+, 59%				
Length of stream	Mar. 1955	D (1 ac)	55	30	14	118	99	3+, 15%				
sections, 0·8 mile								4+, 4%				

TABLE 6 (*Continued*)

Stream	Netting Date (t)	Section Netted*	Marked Fish at End of Netting ($M(t)$)	Fish Captured ($C(t)$)	Marked Fish Re-captured ($R(t)$)	$\frac{M(t).\,C(t)}{R(t)}$	$\frac{\Sigma M(t).\,C(t)}{\Sigma R(t)}$	Age Groups Captured	Mean No. of Fish per ac†	Mean Wt. of Fish Caught (lb)	Wt. of Fish per ac† (lb)	No. of Eggs Produced per ac (estimate)
GROUP 3												
Upper Snowy River	May 1952	A (1 ac)	22	12	2	132	132	0+, 0%	110	0·6	66	30,000
(*Snowy R. system*)	Dec. 1952‡	B (1 ac)	51	30	15	102	106	1+, 4%				
Area netted, 4 ac	Aug. 1953	C (1 ac)	33	30	10	99	103	2+, 72%				
Length of stream	Oct. 1953	D (1 ac)	42	18	7	108	104	3+, 18%				
sections, 3 miles	Mar. 1954‖	D (1 ac)	42	35	8	185		4+, 3%				
	May 1955‖	D (1 ac)	42	26	4	273		5+, 2%				
								6+, 1%				
Jock's Water	Mar. 1954	A (1 ac)	68	38	23	112	112	1+, 9%	105	0·8	84	40,000
(*Clarence R. system*)	Feb. 1955	B (1 ac)	49	40	21	93	103	2+, 51%				
Area netted, 3 ac	June 1955	C (1 ac)	62	52	29	111	106	3+, 28%				
Length of stream								4+, 8%				
sections, 1·5 miles								5+, 3%				
								6+, 0%				
								7+, 1%				

*Sections netted in each stream are designated A, B, C, D. In Lake Canobolas gill nets were scattered over the lake.

†Excludes all fish less than 9 in. caught in Lake Canobolas and Boorolong Creek. In all other streams fish less than 8 in. are excluded.

‡After continuous floods.

§After exceptionally hot summer.

‖Marked fish at end of netting actually much less, owing to natural mortalities.

Andrewartha and Birch (1954) have drawn attention to the rarity of recorded cases of fish dying in streams as a direct result of lethal temperatures.

Affleck (1952*a*) showed that:

(1) Both brown and rainbow trout of small size (5 cm) died at a temperature of 29–30°C within 30 min.

(2) Large brown and rainbow trout (30–33 cm) died when temperatures reached 27–28° and 28–29°C respectively. At these temperatures death occurred within 10–15 min.

(3) These temperatures agreed closely with those given by Embody (1921) and Needham (1938) for the same species in other countries.

These results show that little or no acclimatization by trout to lethal temperatures has occurred in Australia.

Deaths can occur at lower temperatures if other factors are unfavourable. Chief among these factors are low dissolved oxygen, high carbon dioxide, and pollution.

Large brown trout up to 2½ lb were collected from the MacLaughlin and lower Snowy Rivers in February 1951 when the surface water temperatures reached 28·3° and 28·8°C respectively. The temperature at the bottom of a pool 3 ft deep in the lower Snowy River was 27·5°C. Large brown trout were reported dead in the lower Snowy River in January 1946 when the surface water temperature reached 29°C.

These streams contain both brown and rainbow trout, but no small fish of either species and no rainbow trout were found dead although they were definitely present. Since brown trout die at a slightly lower temperature than rainbow trout, it appears that the temperatures were just below the lethal temperature for rainbow trout. Oxygen determinations were not taken but both streams pass over shallow rapids and appear to be well aerated. Pollution was not present. Dead trout have been reported from other streams during hot weather but temperatures were not taken at these times. Such deaths were most likely due to high temperatures, however, since the following temperatures have been recorded on other occasions: Beardy River 28·1°, Furracabad Creek 28·0°, Wellingrove Creek 28·0°, and Boorolong Creek 28·5°C. These temperatures were all recorded in February 1955. At this time a 2 acre section of Boorolong Creek and an acre section of Beardy River were netted and then treated with rotenone, and only three small trout were collected from Boorolong Creek. These streams are inhabited by rainbow trout only.

All the streams which have recorded surface water temperatures of over 28°C are badly silted in places and few deep pools exist.

(*e*) *Creel Census*

Table 7 shows the mean results of the creel census for streams in each group.

The returns showed that 20 per cent. of anglers caught no fish and 65 per cent. caught only a few fish. The majority of the fish were caught by 15 per cent. of the anglers.

On the average each angler fished for 29 hr during the season and caught 6·8 fish over 12 in. and 8·7 fish under 12 in., a total of 15·5 fish.

TABLE 7

1954–1955 CREEL CENSUS DATA

Factor	Group 1	Group 2	Group 3	Total for All Streams	Estimated for All Anglers
Number of licensed anglers				14,824	
Number of creel censuses returned				443	
Returns (%)				3	
Mean number of trout over 12 in. caught per stream	15·5	49·9	60·2	2,915	97,200
Mean number of trout under 12 in. caught per stream	9·8	54·3	147·0	3,836	127,900
Mean number of all trout caught per stream	25·3	104·2	207·2	6,751	225,000
Time spent fishing per stream (hr)	90	200	168	12,040	401,000
Number of legal-size trout caught per stream per hr	0·17	0·25	0·36	0·23	
Number of all trout caught per stream per hr	0·28	0·52	1·23	0·53	
Mean wt. of trout over 12 in. taken per stream (lb)	$2\frac{11}{16}$	$1\frac{13}{16}$	$\frac{14}{18}$	$1\frac{13}{16}$	
Total wt. of trout over 12 in. taken per stream (lb)	42	90	54	5,250	175,000
Estimated wt. of trout under 12 in. returned to water per stream (lb)	5	22	45	1,500	50,000
No. of streams for which data were forwarded	45	30	12	87	

Most trout were caught early in the season, particularly during October, November, and December. Most of the remaining fish were caught very late in the season (late April).

Although there is a paucity of creel data, the available information points clearly to the fact that fewer under-size fish were taken from the good-growth waters than from the poor-growth waters.

IV. Discussion

In Tables 2, 3, 4, 6, and 7 the trout waters are classified according to fish size into three groups, 1, 2, and 3. Streams in group 1 produce the largest trout, group 2 streams produce trout of intermediate size, and group 3 streams produce large quantities of small fish. Plate 1, Figures 1 and 2, and Plate 2 show typical streams belonging to groups 1, 2, and 3 respectively. Although most group 3 streams have sections similar to that shown in Plate 2, these streams also have quieter and less rugged areas in their lengths.

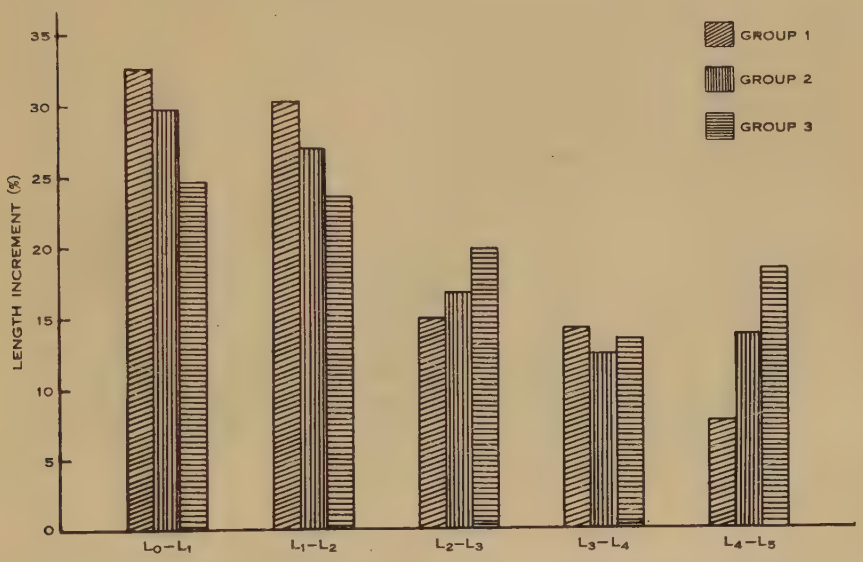

Fig. 5.—The percentage mean increments in length of fish in streams of groups 1, 2, and 3.

It is to be noted that the classification has been made according to size for age and not growth rate. Figure 5 shows the percentage mean increments in length of fish in groups 1, 2, and 3 over a number of years. It is evident that in all years the growth rates of fish in groups 2 and 3 approach or even exceed that of fish in group 1.

The condition of the trout was far superior in group 1 streams, the mean condition factors being 47, 42, and 39 in groups 1, 2, and 3 respectively. If the percentage mean increments in weight of trout in the three groups are plotted, they are greatest in group 1 and least in group 3 in every year except the last (fifth) year, where the position is completely reversed (Fig. 6). This indicates a marked slowing down in growth rate when the trout reaches a length of about 24 in., or a weight of a little over 6 lb. This can also be seen clearly in group 2, where there are data for L_6 to L_7 (Table 4). The percentage mean increments in length and weight are based on the mean length and weight of fish of the same age, 5-year-olds, in each group. Therefore this method is still suitable for making comparison between each group.

The classification into groups would not be satisfactory if it was based on growth rate, but if it is based on age-length, or preferably age-weight, relationship then the classification is clear, as can be seen in Figure 7. The only requirement for placing a stream in a particular group is that in some instances it would be necessary to obtain trout older than 1 year, as there are exceptions to this classification with some trout under 1 year old. A most striking example is that of the Murray River below Hume Weir, where the average L_1 is only 5·9 in. The lengths at L_2 to L_6 are 14·0, 20·1, 23·5, 25·0, and 28·0. The reason for this poor growth in the first year is

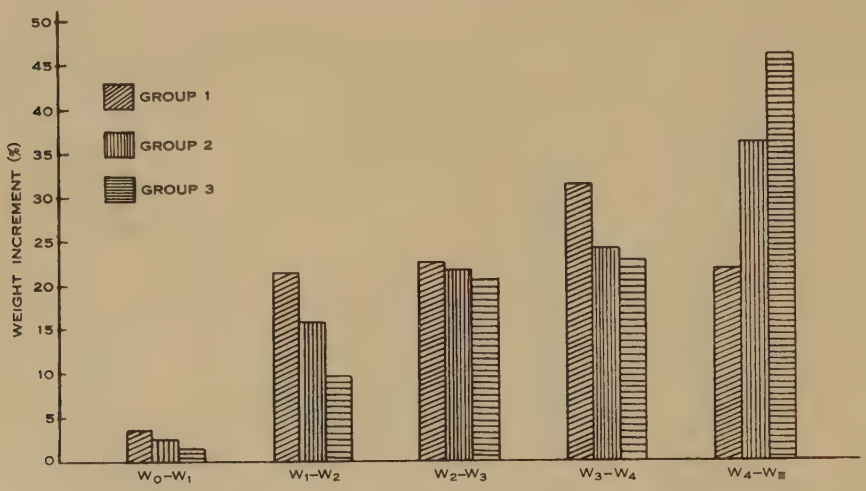

Fig. 6.—The percentage mean increments in weight of fish in streams of groups 1, 2, and 3.

not established, but it is most likely to be caused by the occurrence of spawning in upper tributaries where populations are possibly more dense and growth quite slow. Many of these fish could move down into the Murray River during their first year. It is significant that few fish caught in this area are under 2 or 3 years old.

It is usual for trout in streams of group 1 to be larger as yearlings than in the other groups, yet the percentage mean increments in length are not as good in group 1 in later years. These facts suggest that the smaller size of yearling fish, particularly in group 3, is due to population density or some other related factor such as food, reproductive success, or survival. Figure 8 has been prepared from information in Tables 3, 4, and 6. This shows the relative differences of various factors in each group and supports the suggestion made above.

It has already been mentioned that some streams classified as group 1 may have headwater regions which fit better into group 2, or even group 3. Naturally the extent of the headwater region determines, to a large degree, the conditions in the lower reaches. Table 3 shows that certain chemical, physical, and biological characteristics are common, usually within a restricted range, for each group. For example, streams in group 1 have an alkaline pH value which is usually over 8 and remains fairly stable, and total dissolved solids and total alkalinity are usually of the order

of 400 p.p.m. and 90 mg/l. respectively. There are only seven streams where all three characteristics depart considerably from the mean values given in Table 3. Amongst these are the Lachlan River (below Wyangala Dam), the Murray River (below Hume Weir), and the Marangaroo, Kydra, and Kybean Rivers. The latter three streams are notable for the fact that they are nearly choked with aquatic plants. The former two streams are fed by large dams which contain great numbers of submerged or partly submerged dead trees. These conditions may be responsible for these exceptions. No reason can be given why the other two streams, Spencer's Creek and Styx River, are exceptions.

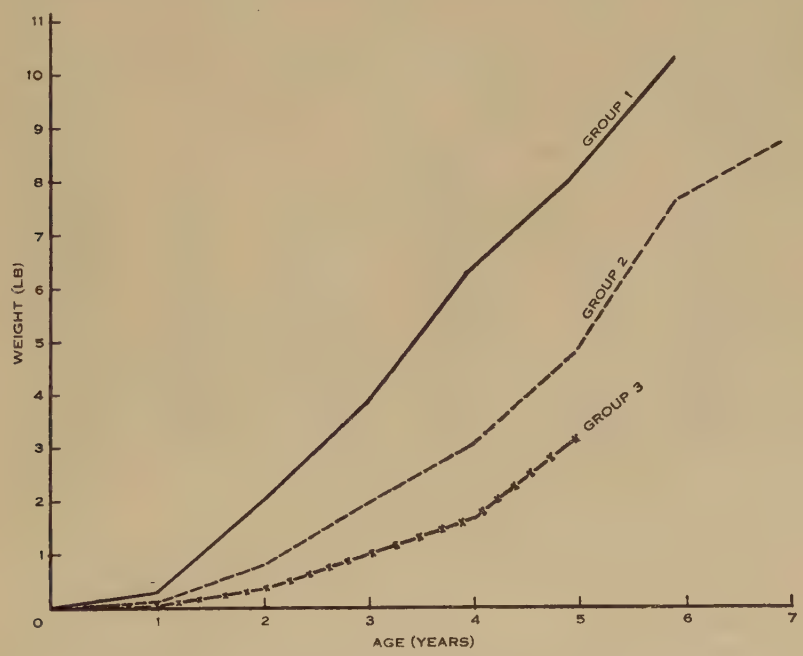

Fig. 7.—Age-weight relationship of fish in streams of groups 1, 2, and 3.

Streams belonging to group 1 are mainly on the western watershed in rich agricultural country. They have a large weight of bottom fauna per acre but are subject to drought, flood, and high maximum temperatures. The topography indicates slow current velocity, and the geology and soil associations indicate unstable stream beds, potential erosion, and chemical nature of the soil (Roelofs 1944; Leeper 1952) which determines the chemical content of the water to a large degree. In addition the major part of these streams is at relatively low altitudes. Consequently these streams are subject to sudden fluctuations in river level and stream bed disturbances, particularly where unwise land usage is common.

These conditions are associated with high water temperatures, to the extent that for a month or two in many years conditions are limiting for trout. This has caused poor fishing and even the complete abandonment by trout of some stretches of some streams during summer periods, as shown in the MacLaughlin River,

Boorolong Creek, and Beardy River (Table 6). Mortalities of fish have been noted in a number of streams when temperatures have exceeded 27°C. Over 70 per cent. of the streams studied have attained temperatures of at least 24°C. Temperatures up to 29°C have been recorded. Where limiting conditions for trout have been found, they can be related to mean air temperatures exceeding 20°C for the hottest month, even though no seasonal drought occurs in the summer-autumn period. In most cases where the mean temperature for the hottest month is under 20°C but there is a seasonal drought period at the same time, then limiting conditions again occur unless the upper reaches of the stream are in a more favourable climatic zone.

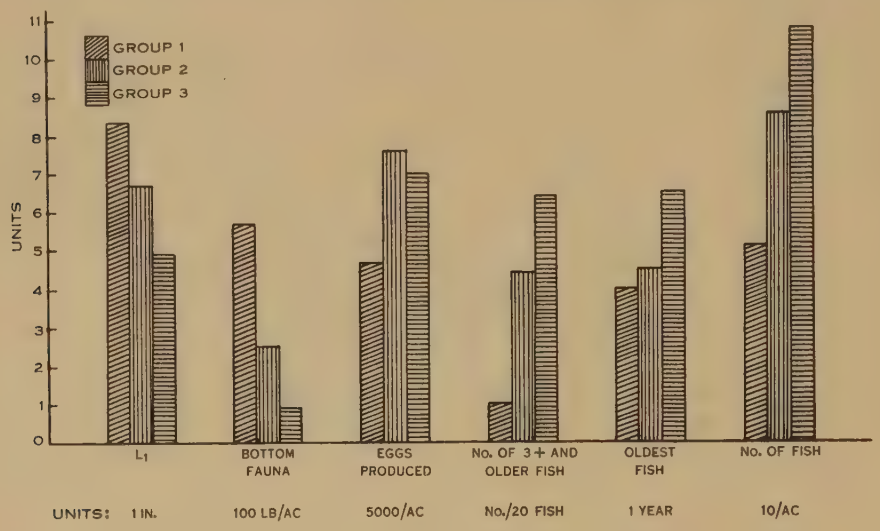

Fig. 8.—Relative differences of various factors in each stream group.

In streams of groups 2 and 3 wide variations from the mean values for pH, total dissolved solids, total alkalinity, and fish lengths at the end of each year, as shown in Tables 3 and 4, did not occur. These tables show that the growth of the fish becomes less from group 1 to group 3 and there is a progressive move to more acid pH, less total dissolved solids, a lower total alkalinity, and a marked reduction in bottom fauna. Faster current velocities, more stable stream beds, and cooler water temperatures are also encountered more often, particularly in streams belonging to group 3.

In streams from group 1, fish over 2 or 3 years old were rarely caught and therefore survival over a number of years was rare. Although the mean age of the trout caught was usually under 2 years the mean weight was relatively large. Also the length at first spawning sometimes exceeded 20 in. and was generally over 14 in. in group 1. This was the case in 42 per cent. of the total number of streams.

In the streams studied it was usual for rainbow trout to spawn at the end of their second year and brown trout at the end of their third year. On some occasions brown trout did spawn when only 2 years old. Male trout often spawned a year

earlier than the females, particularly in poor-growth waters where small, old fish were abundant.

Good growth occurred and fish 5 and 6 years old were present only in areas where temperatures did not become limiting and where conditions of stream bed and flow were fairly stable. An example is the Murray River at Hume Weir.

In about 20 per cent. of streams trout spawned first when less than 12 in. in length. This means that in most streams (80 per cent.) trout first spawned when larger than 12 in.

Trout spawned at the small size of 8·2 in. in Paddy's River, at 8·4 in. in the upper Goodradigbee River, at 8·9 in. in Barrington River, at 8·0 in. in Allan's Creek, and 6·8 in. in Belford's Creek. Although trout may reach 12 in. towards the end of their third winter they will not be available until the open season, when they will have entered their fourth year. This means that trout often had to live until their fourth year in these waters and might have spawned at least twice before they were takable. These waters provided very poor growth conditions, as indicated by chemical and physical conditions, yet they had good spawning facilities. It is possible that they were too heavily populated for the amount of food present.

The results on population studies in Table 6 are not comprehensive but give some idea of the magnitude of the number and weight of trout per acre. Some explanation and discussion on these topics has already been given in Section II (*g*). The indications obtained from the stream surveys are supported by these results. Particularly it is shown that there are few old fish, and even complete disappearance of fish, from some sections of streams such as Boorolong Creek, Beardy River, and MacLaughlin River in hot weather. The relationship between amount of bottom fauna and weight of fish per acre shows a marked difference for each group. For each group Figure 9 shows the weight of fish to every 100 lb of bottom fauna.

The food requirements of trout have been studied in detail by Pentelow (1939). By further analysis of his data it has been shown by Allen (1951) that they need to eat 1·23 per cent. of their weight each day for maintenance, and must have an additional 4·2 lb of food for each pound of growth. It is clear from this and Figure 9 that the food supply may be a limiting factor, particularly in group 3 streams. It also seems reasonable to assume that group 1 streams are understocked and could carry up to twice as many fish and still give growth comparable to the satisfactory growth obtained in group 2. It is not so much the food which is limiting in group 1 streams as the physical conditions.

The streams studied in groups 2 and 3 carried about 100 fish per acre, although weight per acre varied owing to the size of the fish. On the other hand Campbell's River, Boorolong Creek, and Beardy River in group 1 carried less than half this number of fish. The number of eggs produced annually by trout in these streams was also much lower than in streams belonging to groups 2 and 3. In some instances there were as few as one-tenth as many eggs produced. In addition group 1 streams were those which had unstable stream beds and were most subject to flood conditions. Consequently mortalities could be up to 100 per cent. in some areas during continuous severe flooding at spawning time.

It may be argued that the creel census gives no true picture because of the few returns. In particular it may be thought that only the more proficient anglers would send in returns, and thus the numbers caught and rate of catch would be on the high side. Two arguments are available against this hypothesis. Firstly, 20 per cent. of the anglers who sent in returns caught no fish at all; and secondly, a prelimininary analysis of the returns so far received for the 1955–56 season already shows a larger percentage of returns and a larger number of fish captured per angler than the 1954–55 season.

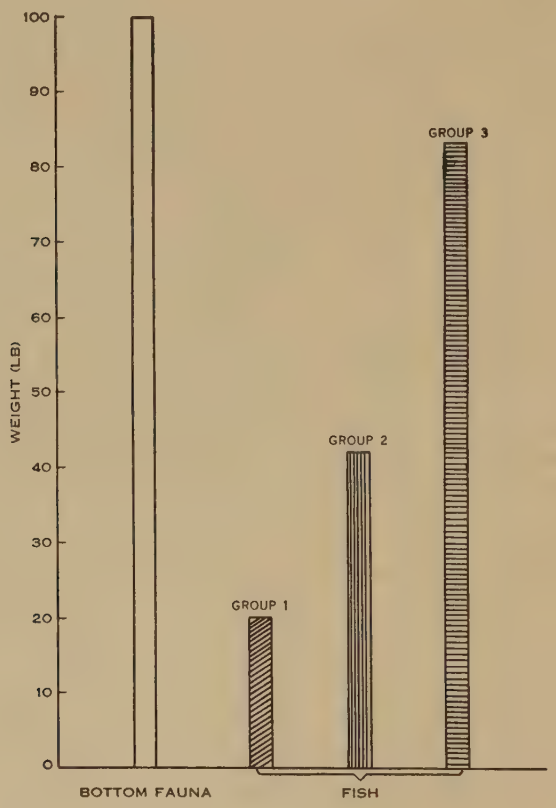

Fig. 9.—Weight of trout per 100 lb of bottom fauna in streams of each group.

On the average each angler took about one fish every 2 hr, although if only those over 12 in. (the minimum legal length) were counted then about one fish every 4 hr was taken.

The fact that the majority of trout were caught early in the season during October, November, and December, and most of the remainder very late in the season (April) indicated that the fish were not so readily taken during the warmer months. The amount of fishing during this period was greater owing to the holiday season.

Table 7 shows clearly that the number of trout below the legal length caught per hour in streams in group 3 was far higher than in the other groups. Even better fishing for legal-size fish was experienced in group 3 streams. These facts also point to the fact that there is greater competition for food in group 3. Group 1 streams provide very poor fishing indeed and unless means of improving them economically can be found it seems useless to persevere with trout in these waters. It is obvious that most group 1 streams would provide better fishing with a species of fish more suited to the environment.

The age composition of the trout caught by anglers differed in groups 1, 2, and 3 owing to the various ages at which the fish reached legal size. For example, in the MacLaughlin River (group 1), about 50 per cent. of the recorded catch consisted of fish 1 to 2 years old and most of the remainder of 2- to 3-year-old fish. In the Tumut River (group 2) about 50 per cent. of the catch were 2 to 3 years old and most of the rest were older. A considerable number were, however, 1 to 2 years old. In the upper Snowy River (group 3), over 70 per cent. of the fish taken were 2 to 3 years old and over.

When the weight of each year class is at a maximum, this class should be taken by the angler in order to obtain the maximum crop, provided that sufficient mature fish are left to spawn to continue the stock. The most desirable kind of catch may of course vary in different fisheries. Allen (1954) pointed out that different conclusions may be drawn as to the optimum value of the size limit for any particular fish stock, according to the particular criterion which is accepted as defining the best catch. Allen considered three distinct definitions of the best catch, which involved quite different requirements. These were:

(1) The maximum total number of fish, independent of size;

(2) The maximum number of large fish;

(3) The maximum total weight of fish.

He shows that for (1) there should be no size limit; for (2) no size limit should be applied if the total catch is restricted by a bag limit and the rate of exploitation is above certain limits; and for (3) the size limit should coincide with the maximum weight of each year class, although in actual practice this size limit would have to be a little less because trout fishing is not akin to complete instantaneous cropping such as may take place in commercial fish ponds.

Further, Allen (1955) shows that, in practice, a bag limit will not give sufficient stabilization to enable the number of large fish caught to be increased by removing the size limit.

The once accepted principle that each fish must be given a chance to breed before it is killed is now generally not believed and has been shown to be inapplicable in many instances, particularly where fecundity is high. Several authors (Surber 1937; Needham, Moffett, and Slater 1945; Schuck 1945; Westerman and Hazzard 1945*a*, 1945*b*, 1945*c*; Needham 1949; Lagler 1952; Cooper 1953; Miller 1953; and others) have pointed out the dubious worth of legal lengths, the enormous natural mortalities which occur particularly in young stages, and the limitations of hatchery liberations.

Nevertheless it is essential to leave sufficient mature fish to spawn in order to continue the stock unless the future supply of fish is to come from the hatchery. This could be decided by either economic or biological considerations, or both. Allen (1954) maintains that insufficient data are available to say what constitutes an adequate breeding stock. However, in the case of New South Wales trout streams the results strongly suggest that in many cases natural breeding is poor, and survival over a number of years is not good, owing to adverse environmental conditions. Irrespective of the number of breeding fish, the environmental conditions pertaining after laying of the eggs determine the number of offspring which survive. The results show that most group 1 streams can be readily affected by adverse conditions. Another way in which breeding may be affected is by temperatures exceeding 15°C for all or part of the last 3 months prior to spawning. This can reduce the hatching of eggs, as shown by Needham and Welsh (1953) in the Hawaiian islands. Unfortunately sufficient data are not available from the present study to show if this is the case in New South Wales, but it quite easily could be.

Trout in 80 per cent. of the streams studied spawn at sizes greater than the present legal limit of 12 in. Seventy per cent. of the streams at times provide conditions which are limiting or near limiting for survival with temperatures over 24°C and in many of these streams natural mortality is very high (Tables 6 and 7). In the 20 per cent. of streams where trout spawn when less than 12 in. there are usually large populations of small stunted fish and over-protection is obviously partly the cause.

If there is any need for a legal limit it is complicated by the fact that the ideal size varies with each stream and even in different portions of the one stream.

Other factors suggest that the legal length would be best eliminated in New South Wales. Two of these factors are eel and cormorant predation.

Although little work was carried out on the eels captured in the streams, it is interesting to look at some results from New Zealand (Cairns 1942; Burnet 1952). The female long-finned eel was the most predaceous; and eels 12 to 30 in., which comprise about 75 per cent. of the eel population, fed mainly on the same members of the bottom fauna as did the trout population and were able to kill and feed on small trout up to 4 or 5 in. The eels of over 30 in. (about 15 per cent. of the eel population) fed to some extent upon the bottom fauna and were quite predaceous on trout. Where the food supply was a limiting factor for a trout population then the eel population would compete with the trout population to a significant degree. This must happen in many group 3 streams. Large eels were capable of swallowing whole trout of 1 to 2 lb. Since eels in many waters probably outnumber the trout population, they are a serious menace.

Cormorants have eaten trout as large as $2\frac{1}{2}$ lb but the majority of fish eaten are usually under $\frac{3}{4}$ lb. As it is not practicable to destroy all or even a large percentage of the eels and cormorants, then a way of controlling them would be to reduce their food supply, that is, the angler could take some of the fish which these predators now eat. It is unlikely that more bottom fauna would be available for eels, because of the limiting food supply in group 3 streams. Direct control of predators does not always

provide the desired effect; bird control in some districts of Canada was almost offset by increased eel predation. Ricker (1952) has treated this problem mathematically, having worked out numerical relations between abundance of predators and survival of prey under various conditions.

It is also apparent that to some extent in group 2 and particularly in group 3 streams, a smaller percentage of the fish available were caught by anglers and a greater number died before the year class became takable, because the legal limit was too high. The angler is not being allowed to make the best use of the available stock, and all the circumstances suggest that the minimum legal length should be eliminated.

The majority of streams warm up so much in midsummer that trout are extremely difficult to catch; where possible, they may move to cooler areas, or even fail to survive. It is evident from creel census and population data that only an extremely small portion of the population is caught by anglers. The open season for trout extends from October to April inclusive. However, the angler can catch few trout during December, January, and February owing to the high water temperatures. It is considered that the open season should be extended to at least September to May inclusive.

In a few areas the spawning of some rainbow trout has not finished by September. A few fish have even been seen spawning in October. It is considered that this matters little, for the following reasons:

(1) Increasing temperatures reduce the chances of the spawning being successful.

(2) The possibility that redds from earlier spawners may suffer interference due to superimposition. Owing to siltation many streams, particularly in group 1, lack extensive suitable spawning areas. Although data are not given to support this view general observations suggest that superimposition does occur. The taking of late spawners could therefore actually increase the number of fry produced, particularly in group 1 streams.

(3) The reduction of spawners in group 3 streams would be an advantage, as competition for food is too great.

(4) Only a fraction of the fish available in the streams are taken by anglers. Natural mortality accounts for most of them.

The only drawback of an extended open season is that some anglers consider that spent fish have not made sufficient recovery by September and do not provide good sport.

The present practice of stocking streams with fry and fingerling trout reared in hatcheries seems to be of little value. There are a few small streams (group 3) in which natural self-maintaining trout populations occur. In these, successful natural reproduction usually results in an over-abundance of small trout. Most of the remaining streams (particularly those in group 1) can give good survival for usually no more than two consecutive years. Although these streams are not really suited to trout they do grow trout quickly, and 4-lb fish can be produced in as little as

2 years. Other evidence available suggests that liberations of 3 to 4 in. trout, which are usually about 6 months old, is wasteful. A total of 23,000 fin-clipped trout of this size were liberated into several streams 3 to 6 years ago, and to date only 0·1 per cent. have been reported captured (Table 5). This also suggests that even streams in group 1 must be self-supporting as regards population. The hatchery is certainly not the angler's panacea for all fishing ills and it is time that their position was put into correct perspective. Experience and tests in the United States have shown that hatchery-reared trout are usually of poor quality and lack stamina, principally because of poor food and feeding.

It is considered that hatcheries could play an important part by providing fish for areas which are suitable, but have no facilities for breeding. Dams and lakes fall principally into this category. Secondly, streams where limiting conditions occur and survival is low over hot dry periods could be maintained as trout-fishing streams by stocking with larger fish. This would only be economic if fishing intensity was sufficient to capture most fish. The hatchery could thus play an important part in these streams where growth is quick but mortality high in hot dry summers.

It is considered that much of the additional information needed for a better understanding of the problems associated with the trout fishery in New South Wales can be obtained by carrying out an experiment over at least a 5-year period. This experiment would consist of liberalized regulations, including elimination of the minimum legal length, extension of the open season, and planting of marked hatchery-reared fish of at least 8 or 9 in. in suitable areas. In addition extension of the creel census would provide much-needed data.

V. Acknowledgments

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The late Professor Harvey Johnston kindly identified *Eustrongylides phalacrocoracis*.

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TROUT IN NEW SOUTH WALES

Fig. 1.—The Beardy River, a typical group 1 stream. Access to rivers by stock has caused destruction of river banks with consequent widening and siltation of streams.

Fig. 2.—The Tumut River, a typical group 2 stream.

Pipers Creek (upper Snowy River), a typical group 3 stream.

THE TASMANIAN TROUT FISHERY

I. SOURCES OF INFORMATION AND TREATMENT OF DATA

By A. G. Nicholls*

[*Manuscript received March* 28, 1957]

Summary

This paper is a general introduction to a series dealing with the state of the trout fishery in Tasmania. Methods of collecting and analysing information are described, and the general scope of the survey is outlined.

The examination of a large number of scales in relation to the length of fish has shown that scales normally appear when the fish are about 3·5 cm in length. They grow rapidly at first and quickly establish a straight-line relationship between fish length and scale length.

Tagging tests carried out on small fish have shown that a large proportion of fish under 14 cm are unable to carry jaw-tags for more than 2 months. This is related to the relative weight of fish and tag in water, when the fish weight is reduced to about one-twentieth of its weight in air, and the tag is thus heavier than the fish.

Experimental work on selective breeding failed to yield significant results, probably owing to nutritional deficiencies associated with hatchery rearing.

The growth of individual brown and rainbow trout in relation to temperature was followed for about 3 years.

I. Introduction

For a number of years there has been expressed by anglers an increasing dissatisfaction with the state of the trout fishery in Tasmania. It has been contended that there is a State-wide deterioration in respect of both the numbers taken and the quality, or condition, of the available fish.

The inland fisheries of this State are administered by the Salmon and Freshwater Fisheries Commissioners, constituted under Part III of the Fisheries Act, 1935. As a result of representations made to that body by anglers' associations the Commissioners, in 1945, requested the C.S.I.R. (as it then was) to undertake an investigation into this question of deterioration.

Little factual information concerning the fishery was available at that time, but a simple system of returns of catches to be made by anglers on the reverse of their licences was established in 1945. Record books were in existence at two of the lakes, but these cannot be regarded as complete returns of catches. Such information as can be derived from them will be referred to in the appropriate places.

This and subsequent papers have been issued in expanded form as a series of Reports to the Commissioners.

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II. Sources of Information

(a) *The Creel Census*

The simple form of return of catches by anglers in use up to the 1948–49 season sought information as to the date of capture, the number and kind of fish taken, and the source. For the 1949–50 season a new form of return, the Creel Census, was issued by the Commissioners, which sought more detailed information from anglers under the following headings: date, kind of fish, sex, length, weight, name of river or lake, locality, type of lure, and number of hours spent fishing.

It was hoped that an analysis of the data provided would yield factual information as to the condition of the fish, as well as to the numbers taken, and that the whole could be analysed for each river or lake in Tasmania in relation to fishing effort, the lure used, and so on, and that a reliable appraisal of the fishery might be made.

This creel census has been in operation from the beginning of the 1949–50 season, and it is intended to publish a series of papers based on analyses of these returns supplemented where possible by additional data accumulated during the 5 years up to 1954. The data derived from the returns of the preceding four seasons are also included.

Although it is still not possible to make comparisons between this period and the preceding decades, it is considered that over the 9-year period covered, any extensive deterioration, if it existed, should have become apparent.

For various reasons it has not been possible to make as complete an analysis as was anticipated. One of the more serious omissions has been that of discovering any change in the condition of the fish. The majority of anglers do not carry spring balances sufficiently accurate to give weights that can be used for a study of condition. It is very clear from an examination of the returns that in many cases the weights given have been estimated and are not the result of careful weighing.

It is clearly desirable in making a study of the fishing effort to discover whether it took longer to catch a fish in 1953–54 than in 1949–50; but it has proved impossible to use these figures because they are not regarded as statistically reliable.

It was hoped that the records kept by anglers would be kept in such detail that every excursion would be recorded, even if no fish were caught. Although some anglers have done this, in many cases they have neglected to state where they fished, or have omitted other vital information which invalidates an analysis from this aspect. In many cases, too, the total number of fish taken over a period of several days has been given and these could not be included in an analysis of the daily catch. Lengths of fish, where given, have been accepted as it is considered that in general these should be reasonably reliable.

One of the major difficulties in assessing these returns has arisen from the relatively small number of anglers who have cooperated. Table 1 provides figures which show that the number of returns has seldom exceeded 2 per cent. of licences issued. The question which arises, therefore, is the extent to which these returns can be regarded as representative of the angling population.

It has had to be assumed that they are representative and while it would seem from the results, which show similar trends throughout, that this assumption is possibly justified, there must remain a very considerable doubt as to their being truly representative. This will become evident in the general discussions.

(*b*) *Field Record Books*

The supplementary data collected to support and extend the analysis of anglers' returns consist chiefly of the collection and examination of scale samples from a proportion of the fish taken.

For this purpose the cooperation of a number of selected anglers was sought, whereby all the fish taken by them would be carefully weighed and measured, and the full data together with a sample of scales from each fish entered in a field record book provided for the purpose.

Many anglers have cooperated in this effort, which has yielded valuable results. Although not all of the weights given by some of these anglers are accurate, it is possible that some indication of condition may be extracted from this limited number of fish.

TABLE 1

NUMBERS OF LICENCES AND RETURNS FROM 1945–46 TO 1953–54

Data	Season								
	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
Licences	3341	3611	4477	5876	7109	8603	9141	8797	8812
Returns:									
Number	66	67	89	42	158	181	119	194	124
Per cent.	1·98	1·86	1·99	0·71	2·22	2·10	1·30	2·21	1·41

(*c*) *Observation of Spawning Runs*

Another source of information has been the spawning runs of fish at the Great Lake, Lake Leake, and the Plenty River, which have been studied for a number of years. The additional data collected thus and by various netting operations will be dealt with in the appropriate places.

III. TREATMENT OF DATA

This series of papers will cover, firstly, the rivers of the north-western region; secondly, those of the north and east; thirdly, those of the southern part of the State; fourthly, the lakes; and finally, a general review of the fishery with conclusions and recommendations.

As much as is necessary of the historical background of the introduction of trout into Tasmania will be dealt with in the final report. It will suffice for the present to state that it has been the custom of the Commissioners to rear increasing

quantities of trout fry, fingerlings, and yearlings for release in the fishing waters. Anglers have come to regard this practice as fundamental to the maintenance of the fishery. On biological grounds, and on the evidence provided by Hobbs (1937, 1940, 1948) based on many years' research in New Zealand waters, this appears to be unsound provided certain conditions are satisfied.

As a result of a statement presented to the Commissioners in November 1951, they agreed to a proposal to cease stocking rivers of the north-western region for a number of years. This subject will be fully discussed in the final paper. The same method of treatment will be used throughout; available data will be presented under the headings given below, for each river or lake where information is available; it will then be summarized for the whole district and discussed in detail.

(*a*) *Statistical Methods*

A short account of the statistical methods used to evaluate the results may be of value. The data showed abundantly the differences in skill of the various anglers. Hence, in estimating the variation of a mean for a river during a certain year two components of variation had to be taken into account: (*a*) variation between anglers, (*b*) variation in the performance of the individual anglers from day to day. The contribution of the component (*a*) to the error of the mean decreases in proportion to the number of anglers, that of (*b*) in proportion to the number of angler-days. As both components of error of the mean were of the same order of magnitude, neither could be neglected.

The number of fish, x, was transformed to $\sqrt{(x-1)}$ before analysis in order to reduce the skewness of the distribution and stabilize the variation. For each river and each year an analysis of variation "between and within anglers" was carried out, from which the components of variation (*a*) and (*b*) were estimated. When the components (*b*) did not differ significantly from year to year they were pooled. The components (*a*) were pooled in any case because the number of anglers was so limited.

In the analysis of the record of angling over a period of 27 years the analysis was carried out on the actual daily catches instead of upon the square root transforms. The analysis of variation was made within and between years for both fresh and tidal waters. To detect trends in the yearly averages, curves were fitted through them, which were built up as the sum of the constant, linear, quadratic, cubic, and quartic components, which were fitted successively until the main part of the significant variation was accounted for. The catch in fresh water required to be taken only to the quadratic; that in tidal waters was taken to the quartic, at which stage there still remained a slightly significant variation.

The standard method of estimating the variation between the fish length means was used in all cases. Where differences are stated to be not significant, this indicates no statistical significance at the conventionally accepted 5 per cent. level. Where they are stated to be significant, without further qualification, this indicates significance at the 0·1 per cent. level. In other cases of significance the level is given in the text.

Regression equations were calculated by the method given by Snedecor (1938, p. 102).

(b) *The Daily Catch*

Anglers' returns are analysed in respect of the individual catch per day for each season, and the results, expressed as the mean number of fish per angler per day, are compared for any changes over the period of nine seasons. For the last five of these, information is available which enables the catch to be analysed according to whether the fish were taken in tidal (estuarine) waters or above (fresh, inland).

This mean value for catch per angler per day has been subjected to statistical treatment to determine the significance of seasonal differences. It should be noted that all records of no fish per day have been omitted from the means, since it is certain that only a small proportion of returns includes such values, and during the earlier years no returns included nil catches per day. This omission, which will give a somewhat higher value to the means than is actually the case, will make these figures reliable for comparative purposes, which would not otherwise have been the case.

In a number of cases the data from any one river are too scanty to yield reliable conclusions.

(c) *The Size of Fish*

Returns are analysed in respect of the size distribution of fish taken over the last five seasons, during which lengths were recorded by the majority of anglers making returns. It has been necessary to separate fish from tidal and fresh waters throughout, owing to the difference in the legal minimum length which operates in each.

Owing to the difficulty of delimiting tidal waters, for purposes of the angling regulations an arbitrary boundary has been fixed by the Commissioners, indicated by posts set up at specified points in each river. Below the boundary fish less than 12 in., measured from the tip of the snout to the end of the central ray of the tail fin, must be released; above the boundary the minimum length now operating is 9 in. Prior to the 1951–52 season the length was 8 in. (for brown trout); as a result it has been necessary to omit all fish below 9 in. in making a comparison of the size of fish over the period.

Measurements of fish recorded by anglers were given to the nearest $\frac{1}{4}$ in. For convenience in treating the data sizes have been grouped in 1-in. groups, at integral centres, $\frac{1}{2}$-in. values being allocated to the group above. This will also serve to counteract possible inaccuracies in measurements. In certain waters, notably lakes, a 14-in. size limit operates.

This analysis of size has been made to discover any change from season to season because, concurrent with any depletion of the stock due to overfishing (or understocking), firstly, there would be a decrease in the average size of the fish taken due to the removal of the larger fish and the increased fishing pressure on the younger fish, and, secondly, the reduction of the population would probably bring about an improved growth rate due to the reduced competition for food. While it is possible that these two factors might counteract one another, it is unlikely that one would exactly offset the other and produce stability, but in any case a study of the growth of the fish as shown by their scales would show if there had been any change.

Moreover, if the fishery depended on the release of hatchery-reared fish to maintain the stock, a view still held by a proportion of anglers, the cessation of this practice in the rivers of the north-west from 1951 onwards would have resulted in a rapid decline in the numbers taken, an increase in the average size following the reduced competition for food, and a very extensive elimination of fish of the younger age groups. The last is self-evident, and it follows that if the contribution made by hatchery releases is of any real significance then the proportion of young fish in the catches should have changed during the years following the cessation of stocking.

(*d*) *The Age and Growth of Fish*

The various problems associated with the determination of the age of fish as revealed by their scales are well known and have been discussed by various workers. Allen (1951, p. 113), for example, has expressed the opinion that scale reading is highly subjective and that the variations in the spacing of the circuli or the possible absence of one or more winter rings may lead to erroneous conclusions without supporting evidence on the growth rate derived from other sources. This is very clearly so in the Horokiwi, where growth during the first 12 months, as shown in his Tables 38 and 39, is steady and shows no slowing down during the winter. This results in a greater length at the end of the first year than normally occurs in Tasmanian waters, which may be related to temperature differences. The mean monthly range given for the Horokiwi was from 7·5 to 19·5°C, whereas the comparable range in the Plenty River is from 3·5 to 19·5°C.

The experimental work of Gray and Setna (1931) and of Bhatia (1931, 1932) has shown clearly that the formation of wide and narrow rings in the scales of (rainbow) trout is not related directly to temperature but to the food supply, from which it may be assumed that the scales reflect the growth of the fish. Bhatia (1932) noted that fish kept at 4°C for the period of the experiment showed less inclination to take food than those at higher temperatures. It is of interest to note that the fish in his control tank (in which the temperature varied from 7·5 to 14·5°C), fed at a uniform rate, showed no periodic zones on the scales. This suggests that where winter temperatures do not fall below 7·5°C, as in the Horokiwi, growth is likely to be continuous and the scales may show no winter rings, provided the food supply is adequate.

The data presented by Allen (1951, Appendix II) show that there was relatively little variation in the total weight per unit area in the bottom fauna during 1940, and the winter values (June and August, at times of minimal temperatures) showed no tendency to be lower than summer values in any zone in the Horokiwi. (The 1941 values were influenced by serious flooding.) This, and the comparatively high minimal temperature, would seem to provide suitable conditions for continuous growth. No comparable data are available for the food supply in Tasmanian streams, but it has been observed that at times of lower winter temperatures hatchery trout become sluggish and show little inclination to feed. It may be concluded that the more marked difference between summer and winter conditions here will influence their feeding, if not their food supply, so that winter rings in river fish are clearly marked.

Difficulties in scale reading have been encountered occasionally. False winter rings are usually identifiable by their short duration, interrupting the span of normal summer growth; these can safely be ignored. In the case of fish from some of the Tasmanian lakes some difficulty has been experienced over the obvious omission of one or even two winter rings, but with the great majority of stream fish the scales can normally be interpreted with considerable confidence. The scales from fish of known age taken from the hatchery have been examined on many occasions and have shown no evidence of a false first winter ring. Scales from similar jaw-tagged fish not only show their age correctly but also show a mark corresponding to their length at tagging, at which point, it is presumed, feeding has been interrupted for a short time. Scales from marked fish of known age released into streams and later recaptured have provided confirmatory evidence.

Samples of scales taken from fish by the groups of selected anglers have been studied and from these, which were taken in three of the past five seasons, it has been possible to discover the numbers and size range of the fish in each age group. These figures are used to distribute the fish taken by anglers as a whole into their respective age groups, and thus to discover if there has been any change in the age distribution of the population over the past five seasons. At the same time it has been possible to study the growth of fish from different sources over the period. It has not been possible to make this analysis for each river separately owing to the small amount of data in some cases.

The technique of scale reading to determine the age and growth of fish is now so widely used that it is unnecessary to describe the whole in detail. However, it may be advisable to describe some modifications of the apparatus and method used here.

Scales were usually cleaned and mounted by the methods described by Lindsay and Thompson (1932), but when long series of scales had to be examined temporary mounts in water were used.

The general principle was followed of projecting an enlarged image of the scale onto an adjustable screen marked with a graduated scale, using a modification of the apparatus described by Kesteven and Proctor (1941), in which a circular screen pivoted at its centre was used, so that the graduated scale could be aligned with the long axis of the fish-scale image.

The question of the relationship between fish length and scale length has been considered by many workers for numerous species of fish. A summary of the position has been given by Nall (1930, pp. 46–50) who discounted Lee's phenomenon, but without producing very satisfactory evidence.

Apart from the work of Lee (1912) based on Dahl's data no attempt appears to have been made to approach this question fundamentally for trout, and students of age determination and growth in trout appear to have accepted Lea's (1913) rebuttal of Lee's hypothesis, although in a later paper (1920) Lee reviewed the question and maintained that the fish length and scale length are not proportional but that "only the increments of growth of each in the same periods are proportional to each other".

In order to discover the true relationship between the growth of the fish and its scales in trout, measurements were made of 3869 scales from 755 brown trout ranging in size from 6 to 33 cm, taken by electro-fishing in the North Esk and St. Patrick's Rivers in December 1954 and January 1955. The results are shown in Figure 1, from which it will be seen that for this size range, while there is some

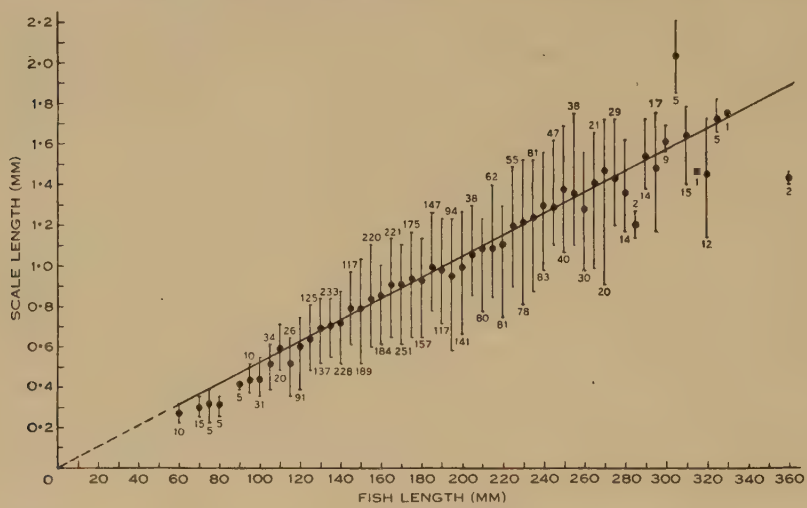

Fig. 1.—The fish-length : scale-length relationship for brown trout from natural sources, ranging from 60 to 360 mm. Mean values only are plotted, but the range of scale length for each fish length is shown by the vertical lines; the number of observations at each fish length are shown on the graph.

spread in the data with occasional samples lying some distance from the mean, the general distribution is such that a straight line gives the best fit. The regression equation for these figures is:

$$Y = 0{\cdot}00519X + 0{\cdot}002,$$

in which X is the fish length (mm) and Y is the scale length (mm). From this it is clear that the extrapolated line passes very close to the origin (when $Y = 0$, $X = -0{\cdot}385$). Thus it would appear that in trout at least there is a clear correlation between fish length and scale length and that they are directly proportional. However, the data on which this regression was calculated can be separated into two parts: those derived from fish from the North Esk and those from fish from the St. Patrick's. These are sections of the same river system and essentially similar, yet the data for the North Esk (1697 scales from 378 fish) yielded one equation ($Y = 0{\cdot}00545X - 0{\cdot}057$), and that from the St. Patrick's (2172 scales from 377 fish) yielded a different equation ($Y = 0{\cdot}00490X + 0{\cdot}061$), and this difference is statistically significant.

These equations are not very different, yet in the first case the extrapolated line cuts the X-axis at 10·5 mm and in the second it cuts it at $-12{\cdot}4$ mm. It is only when the two are combined that these differences cancel out and the extrapolated line passes close to the origin.

The significance of this would appear to be that regression lines based on small samples are likely to be only approximate. In this may lie the explanation of the various positions at which the extrapolated lines cut the X-axis in the different species dealt with by Lee (1920), although all the values were positive. Lee does not state the numbers of scales measured, but it would appear from her Table II that only one scale was measured from each fish since both fish and scale measurements numbered 200.

It would seem perhaps that too much importance has been placed in the past on the point at which the X-axis is cut, and Lee's statement that the position at which this axis is cut indicates the approximate fish length at which scales first appear is, of course, incorrect as is clearly shown below. However, this does not entirely dispose of the problem since Blackburn (1950) claims a differential relationship in fish above and below 6 cm for *Engraulis australis* (White). Since none of the trout taken from the above sources was less than 6 cm it was necessary to use fish from the hatchery at Plenty in order to discover whether such a change occurs in trout.

Scale measurements (251) were made on a sample of trout raised at the hatchery in 1948–49 covering a size range from 3·6 to 9·9 cm and these yielded the equation

$$Y = 0{\cdot}00463X - 0{\cdot}079,$$

which cuts the X-axis at 17·1 mm. While the slope of this line is not very different from that for fish taken from the rivers, its height above the X-axis is quite different. A second series of 982 scales taken from 99 fish measured at the hatchery in March 1956, ranging from 3·2 to 8·4 cm, gave the equation

$$Y = 0{\cdot}00483X - 0{\cdot}098,$$

which cuts the X-axis at 20·3 mm. These two sets of data yielded results so similar that they have been combined to give the equation

$$Y = 0{\cdot}00479X - 0{\cdot}095,$$

and the results are plotted in Figure 2.

It is clear that there is a striking difference in the fish-length: scale-length relationship as between fish from 3 to 10 cm from the hatchery and fish from 6 to 33 cm from the field. These, however, are consistent in that each shows a straight-line relationship and there is no tendency for the slope of the line to change below 6 cm or at any other point. In other words, to quote Tate Regan (*fide* Nall 1930, p. 50): "The scales are formed rapidly and after a very short interval overlap each other to the same extent in quite young fish as in adults".

This difference between fish from the two sources means that fish reared in the hatchery have smaller scales than fish of the same size which have lived under natural conditions. The relative figures over the comparable range of fish lengths are given in Table 2.

Although these differences may be in part due to the small numbers of fish available from natural sources (the numbers ranged from 5 to 31) they are mathematically quite significant except in the case of the 80-mm group, and must be regarded as real.

There must be some explanation for this difference and it is tentatively suggested that the cause lies in the difference in origin, and that rearing under artificial conditions in the hatchery with the fish crowded together and fed on un-

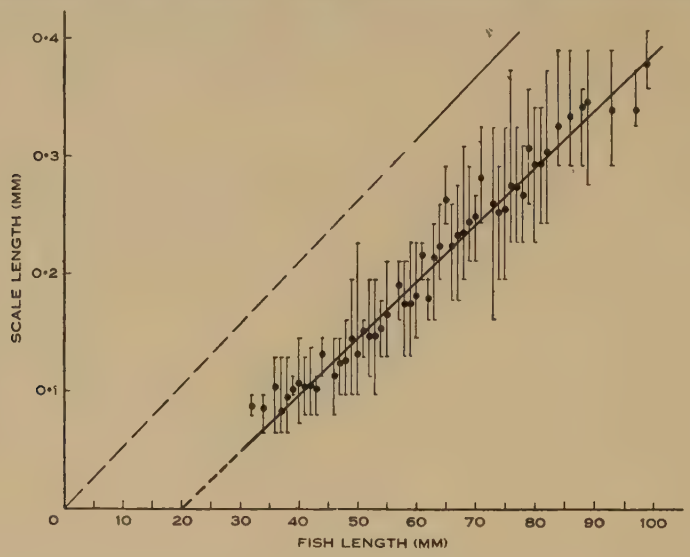

Fig. 2.—The fish-length : scale-length relationship for brown trout from the Plenty hatchery, ranging from 32 to 99 mm. Mean values only are plotted, but the range of scale length for each fish length is shown by the vertical lines. The number of observations for each fish length ranged from 3 to 78, with an average of 9·6, and only 13 sets of data were below the average. The regression line for the data from fish from natural sources, shown in Figure 1, is included to show the similarity in slope.

natural food plays some part. In support of this suggestion it may be pointed out that of the fish taken in 1948–49, random samples of which were preserved in formalin at intervals, scales were first found in fish of 3·6 cm preserved in December some 3

TABLE 2

MEAN SCALE LENGTH (MM) IN FISH FROM DIFFERENT SOURCES

Source	Mean Fish Length (mm)								
	60	65	70	75	80	85	90	95	100
Hatchery	0·180	0·226	0·242	0·263	0·290	0·328	0·343	0·337	0·376
Natural	0·273	—	0·300	0·320	0·316	—	0·413	0·432	0·436

months after hatching, and no smaller fish had scales. These scales consisted of the initial platelet with a diameter of about 0·065 mm. If the straight-line relationship between fish length and scale length holds under all conditions, scale formation

should be a function of size and not of age. Yet in the sample of fish measured in March 1956, some 6 months after hatching, scales were found on the smallest fish available, 3·2 cm, in which none of the scales consisted of fewer than two circuli, or was smaller than 0·081 mm.*

At first sight this appears to support Molander's discovery (quoted by Lee (1920, p. 21)) that in herring of different ages but similar lengths the older herring have larger scales than the younger. This is so in the case of the two trout quoted here but the larger scales in the older and smaller fish were so because they were older scales, consisting of not less than two circuli. Thus, in reality, this shows that if the growth of fish is retarded owing to unfavourable circumstances, scale formation will take place even though the fish is smaller than the size at which scale formation normally occurs.

This probably has some bearing on the relationship and is worth further investigation, but for the present purposes it is sufficient to assume that under natural conditions growth of the scale is exactly proportional to growth of the fish throughout life, and that the initial lag between hatching and deposition of the first platelet is rapidly made good, probably by the time that the second or third circulus is formed. This can be clearly seen in the structure of the scales, since the first platelet has an appreciable diameter (0·065 mm) and the spacing between the first two or three circuli is greater than that between those immediately following, indicating a rapid overtaking of the initial lag (Plate 1). Since there must be a change in the relationship between lengths of fish and scale over this short period, it should be possible to demonstrate it with sufficient measurements over the critical period, of scales carefully taken from exactly the same position on a series of fish, but the data here available do not show it.

In all scale readings of fish dealt with in this series of papers (apart from the very small fish discussed above) the fish lengths were adjusted, and all intermediate lengths were read, to the nearest 0·5 cm.

This degree of accuracy is regarded as sufficient in view of the nature of the original data. Where fish were measured by members of the Commissioners' staff or by Divisional field officers during spawning runs or netting operations, the fish were always alive and the error of measuring such fish lies within a range of about $\pm 0{\cdot}5$ cm. In the case of anglers who recorded fish lengths with their scale samples these were probably most often measured some time after death, when some shrinkage is likely to have occurred owing to drying out.

The age of each fish and its length at the end of each winter having been determined, the results were grouped according to age, and mean values obtained for all fish in each age group. These will be expressed as "mean length-for-age" in the

*All scales were taken from that part of the fish from which it is customary to take scales for age determination in trout, namely, midway between the back of the head and the front of the dorsal fin and equidistant between the dorsal and lateral lines. References to scales first being found in fish of certain lengths are to scales found in this position and do not in any way conflict with the excellent account of the early formation of scales in brown trout, given by Paget (1920). This author stated that the appearance of scales was a function of size and not age, but quoted cases of retarded scale development. The present case is one of "premature" scale development under conditions of retarded growth, so that age must also have some influence.

tables of scale readings. It will be seen that occasionally there is some variation in the mean lengths-for-age in fish of different year classes. It sometimes happens that there tends to be a reduction in the lengths of fish at each year from younger to older fish, which might be regarded as evidence in support of Lee's hypothesis, but it will be seen that this is not constant, and may be completely reversed.

This variation could be real and due to natural fluctuations in the environmental conditions in the rivers from one year to another, or it could be due only to the effect of having small numbers of fish in any particular age group.

In most cases the mean values at any one year, for fish in different year classes, are very close and statistical tests have shown that it is clearly safe to average these results. This has been done and is called the grand mean (G.M. in tables). In calculating the grand means, fish of the 2+ age group in tidal waters, and those of the 1+ age group in fresh waters, have been excluded throughout. There are two reasons why this has been necessary.

Firstly, since the fish of these age groups approach very closely in length to the legal minimum applicable in each case it follows that such fish taken by anglers will not be representative of their age group, because the smaller fish will have been released as undersized. In other words, only the quicker-growing fish of the 2+ age group in tidal waters will have been large enough to reach the legal minimum of 12 in., and similarly not all the 1+ age group in fresh water will have reached the 9-in. minimum.

Secondly, because of the operation of these minimum lengths there is some risk that fish which were close to but did not attain the minimum length will have been retained and recorded as within the legal minimum. These will have unduly elevated the numbers taken and the mean lengths for these age groups.

The first of these factors will operate both in lengths given in the creel census and in the field record books of scale samples; the second is likely to have occurred, if at all, only in the creel census returns. It has had to be assumed that the samples of fish recorded by anglers were representative of the populations of takable fish.

(*e*) *Mortality*

The fish taken by anglers having been allocated to their respective age groups, it follows that simple calculations will reveal the mortality rates in operation from one year to the next. There are insufficient data to provide reliable mortality rates for each river, and this subject will be considered when summarizing the results for the region as a whole.

(*f*) *Tagged and Marked Fish*

One very good method of assessing the contribution to the fishery made by releasing fish from hatcheries is to mark all such fish, either by the application of tags or, more simply, by the removal of a fin. The former is considerably more laborious and time-consuming and has the added disadvantage that a proportion of the tags will not hold on yearling fish; the latter method is adequate when the fate of individual fish is not required to be followed, and, being quicker and easier

to carry out and giving equally reliable results when only numbers of fish are required to be known, this method has been employed on several occasions, supplemented by a proportion of tagged fish.

The numbers of these appearing in the spawning runs in successive years yield information as to the mortality rates, and the proportion of them appearing in the catches in their appropriate age groups provides direct evidence as to the value of hatchery liberations. For the full value to be derived from this method of assessing the contribution from hatcheries it is important that as complete as possible a return should be made of *all* fish taken, and that those which were marked should be indicated.

It is clear from the poor response from anglers that this approach would yield little or no result where it was dependent on anglers' returns. It has therefore been restricted in the main to the Great Lake, Lake Leake, and to a lesser extent the Derwent River, since in such places it has been possible to recapture representative samples of fish during the spawning runs. Fishing by means of an electric current, however, has made possible the recapture at a reliable level of marked fish released into a population. Small numbers of fish have been taken from estuaries by seine nets, tagged, and released in order to discover if there was any movement of fish from one river to another. Larger numbers of fish taken on the spawning runs referred to above have been tagged for growth studies. A number of tagged yearlings from the hatcheries has also been released in these waters.

Apart from a small number of tags specially designed for small fish, the strap tag was used throughout this work. This is made in three sizes and all were used according to the size of fish being tagged. Because of the marked success with which trout remove tags fixed to the operculum, by rubbing them against fixed objects, this position of attachment is useless. Shetter's (1936) method of attaching the tag to one side of the lower jaw was adopted. This author described his method of rounding the tags after application to permit growth of the bones and prevent the tags from being pushed off. He found that in rainbow trout from 8 to 12 in. in length the tag held quite well for 1 year.

A test was carried out to find the lower size limit at which trout could be successfully tagged. In October 1947, 964 yearling brown trout ranging from 7·7 to 14·4 cm were tagged by Shetter's method, and held in the rearing ponds at the Plenty hatchery. Two months later only 450 still held their tags and these were roughly divided into two parts, one of which was transferred to a lake; the subsequent fate of these is unknown owing to the difficulties of recapture.

Table 3 shows the percentage size distribution of the original 964 fish at tagging; of the original lengths of a sample of 213 which were removed from the rearing ponds after 2 months; and of 112 which still held tags 11 months after tagging.

It will be seen that there was a complete elimination of all fish which were less than 10 cm when tagged, and that there was an increase in the proportions of fish in the larger size groups which held tags up to nearly a year. The 11-cm group comprised 38·5 per cent. of the tagged fish, but only 25·8 per cent. of those holding tags for 2 months, and only 20·5 per cent. of those holding tags for 11 months. For

fish 12 cm and over at tagging this trend was reversed and is most strikingly seen in the 13-cm group. There were only 15 fish in the 14-cm group and more than half of these were removed from the ponds after 2 months, so that they were not truly represented at 11 months. It would appear that it is possible to tag fish of 13 cm and over with a reasonable degree of success.

TABLE 3

SIZE OF FISH AND ABILITY TO CARRY JAW-TAGS

Size Group (cm)	At Tagging		After 2 Months		After 11 Months	
	Number	Per Cent.	Number	Per Cent.	Number	Per Cent.
8	4	0·4	0	0·0	0	0·0
9	12	1·2	0	0·0	0	0·0
10	89	9·2	6	2·8	3	2·7
11	371	38·5	55	25·8	23	20·5
12	363	37·7	106	49·8	54	48·2
13	110	11·4	37	17·4	29	25·9
14	15	1·6	9	4·2	3	2·7
Total	964	100·0	213	100·0	112	100·0

It was noted during the first 2 months while the fish were in the rearing ponds that they tended to take up an almost vertical position in the water, with their heads close to the bottom, and to gyrate in this position. This was undoubtedly due to the relative weight of tag and fish in water, and some data on this are presented in Table 4.

TABLE 4

WEIGHT OF TROUT AND TAGS IN AIR AND WATER

Length of Fish (cm)	Weight of Fish		Volume of Fish (ml)	Weight of Tag		Wt. Ratio Tag/Fish in Water
	In Air (g)	In Water (g)		In Air (g)	In Water (g)	
7·7	4·650	0·235	4·7	0·480	0·401	1·7
8·4	5·625	0·295	5·7			1·4
9·6	8·600	0·375	8·3			1·1
11·7	15·670	*c.* 0·69	15·9			0·6

Four small fish were stunned by a blow on the head and carefully weighed in air and in water, being suspended from the balance with thread. Volumes were measured approximately by displacement. Ten tags were weighed in air and in water to overcome any variation in the weight of individual tags.

It will be seen that in the case of the smallest fish, while the actual weight of the tag is only about one-tenth of the weight of the fish, when they are immersed in water the tag is more than $1\frac{1}{2}$ times the weight of the fish. It is surprising that any fish of 9 or 10 cm could adjust themselves to the burden.

This difference becomes increasingly less important as the fish grow, and in older fish tagged with medium or large tags the weight of the tag was relatively insignificant. It will be seen that a fish loses approximately 95 per cent. of its weight when in water so that one weighing 1 kg would weigh about 50 g in water, and a medium tag weighing 1·71 g in air and 1·52 g in water would not constitute a serious burden. The weight of the largest tag was 2·63 g in air and 2·33 g in water.

The result of the prolonged assumption of the near-vertical position together with the freedom of movement given to the rounded tag was that it gradually moved forward along the lower jaw and finally cut through between the two halves and fell off. Many of the fish which had lost their tags in this way survived and were recognizable by the "crossbill" effect of the two halves of the lower jaw. Such fish did not appear to suffer any disadvantage and grew almost as well as those which held their tags. The mean length of all fish tagged was 11·9 cm. At 11 months from tagging the mean length of fish which held their tags was 22·0 cm and of those which lost tags 21·2 cm; the corresponding weights were 113·7 g and 99·2 g, giving condition factors of 1·07 and 1·04 respectively. Statistical test shows that for both length and weight the difference between these means was significant only at the 5 per cent. level. Since the fish which lost their tags were almost certainly smaller when tagged than were those which held tags it is doubtful if there is any real difference. The mean length of some 1500 fish without tags kept in the rearing ponds with the tagged fish to act as a control was 21·4 cm, which indicates that despite the disability from which the tagged fish suffered their growth was not affected.

It appears that rounding the tag when affixed to the jaw is unnecessary, since the metal is sufficiently tough to resist pressure from the growing jaw and subsequent recoveries have shown that the tag tends to become embedded in the tissue rather than to be forced open. Rounding of the tag is also undesirable because the freedom of movement prevents rapid healing around the point of insertion. Experience has shown that even with the larger sizes of tags one which is left unrounded with little or no freedom of movement will soon heal into position provided the fish is in good condition, whereas the rounded tag maintains an open sore on the jaw. It is no disadvantage if the tag when applied pierces the bone as this helps to keep it firmly in position.

(*g*) *Releases from Hatcheries*

An additional approach which will throw some light on the value of hatchery releases is provided by the figures for the known rates at which rivers have been stocked in the past. It is possible to arrive at approximate figures for the estimated total annual catch for each river. Mortality rates applicable to Tasmanian rivers have been discovered, and these in conjunction with the numbers of fry or yearlings released will yield the approximate numbers surviving for anglers.

The relationship which the total annual catch from any one river bears to the estimated survival of hatchery-released fish will further establish the value of this practice.

(*h*) *Condition*

This is normally expressed by the condition factor (K), or length-weight relationship. There are several methods of calculating this factor, depending on the measurements used. Throughout this investigation the standard formula

$$K = \frac{100W}{L^3}$$

has been used, in which W is the weight (g), and L is the length (cm) measured from the tip of the snout to the end of the central ray of the tail fin.

Hile (1936) discussed condition and the relation between length and weight (pp. 237–49), reviewing objections to it on the grounds of inaccuracy. The following paragraph quoted from this author is particularly significant: "Clark's conclusion that the failure of the cube law to describe the length-weight relationship makes inaccurate the use of coefficients of condition (weight-length factors) based on the cube relationship is scarcely justifiable, particularly in view of the fact that coefficients based on empirical exponents fail to reflect differences in form or relative heaviness while those based on the cube relationship offer a direct measure of relative heaviness independent of general length-weight relationships and comparable as measures of relative heaviness between fish of any length." (p. 240).

It may be added that the cube relationship also presents a direct means of comparison between fish of any species, whose average K values may lie considerably above or below unity. The only effect of using a coefficient based on empirical exponents is to bring the average for any particular species to unity (using the metric system of length and weight). There is little value in this since it removes the possibility of direct interspecific comparison and does not overcome the disadvantage inherent in both methods, that of seasonal variation within a species due to gonad development or to other causes.

Klak (1941) discussed the use of this formula and gave the conversion factor for interchanging between the British and metric systems of measurement:

$$K_{(m)} = K_{(Br)} \times 0{\cdot}02768.$$

It has also been discussed by Le Cren (1951) and by Allen (1951). The latter used the cube relationship in his study on trout and it would appear preferable to adhere to this for purposes of comparison.

It is obvious that the use of a condition factor as a means of comparing fish from different places, taken at different seasons or at different times of the day, cannot be regarded as more than a rough guide, because of the varying degrees of development of the gonads and variations in the quantity of food in the stomach, both of which will affect the weight.

For the reason given above the weights of fish as given by anglers in their returns of catches have not been used. However, the importance of accurate weights

was stressed to those anglers who undertook to collect scale samples, and in the majority of such cases the weights given appear to be reasonably accurate.

The weights and condition factors derived from them will be given in the tables setting out the results of scale readings. The original measurements were in British units and these have been converted to the metric equivalents, rounded to the nearest 10 g for larger fish and 5 g for smaller fish, and the K value calculated for each fish. The values given in the tables are the means of the individual values. On those occasions on which fish were netted for tagging, or during spawning runs, the lengths and weights were accurately determined. Mean K values are tabulated for these fish.

(*i*) *Type of Lure*

An analysis of the relation between type of lure used and number and size of fish taken will be included in the final paper of this series.

IV. Biometrical Differences between the Sexes

In the fish caught by anglers there does not appear to be any significant difference between the sexes as regards length, and for most of the year there is no appreciable difference as regards weight. Differences in weight become apparent as the spawning season approaches, and immediately after, and such differences are of course reflected in the condition of the fish. Since the fishery is closed to anglers during the spawning months this difference can be ignored. In those cases where spawning fish have been studied the differences between the sexes will be considered.

Examination of a sample of 164 fish (108 females and 56 males) taken by one angler from the same stretch of river throughout one season showed no significant difference between the sexes as regards length, weight, or condition. The data were then pooled and analysed by months and again no significant differences were found in these respects as between months of capture, neither was any significant seasonal difference found between the sexes. It is probable that many anglers have considerable difficulty in determining the sex of fish, particularly the smaller river fish, and this fact supported by the findings of the statistical analysis justifies the decision to treat all fish together without separation into sexes.

At the same time it is not claimed that no difference exists either between sexes or between months of capture, for it is clear that growth of fish and development of gonad are gradual and continuous processes, which must result in real seasonal and sexual differences. Fish taken early in the season, following spawning, show a poorer condition and later fish show recovery. It should be emphasized that it is only for the purpose of the present comparison of fish from anglers' catches that the data are pooled, because these differences are not statistically significant in these samples.

One reason for the absence of any significant difference from month to month during the fishing season is that, as the season progresses and growth takes place, fish which at the beginning of the season were below the legal minimum begin to enter the fishery in the latter half of the season and so lower the average length and weight of fish taken at that time.

V. Growth and Reproduction in Hatchery-reared Fish

The normal practice when stripping fish for hatchery rearing as carried out by the staff of the Salmon and Freshwater Fisheries Commissioners is to strip a number of females into a clean bucket, to add the sperm from one or more males, and after a few minutes to wash the fertilized ova, which are allowed to harden and then packed in trays with moss for transport to the hatchery. Sometimes the males are stripped first. Fish are taken as they come so that a cross section of the population is represented in the resulting offspring.

Hatchery-reared fish are normally fed on finely ground cooked ox liver, with or without added biscuit, occasionally varied with raw liver; this deprives the fish of much of their essential vitamins. A little natural food will enter the hatchery with the water supply but the quantity must be insignificant while the fry are in the troughs. As soon as possible after hatching the majority are released in fishing waters, but as many are normally retained for rearing to fingerlings and yearlings as can be accommodated in the rearing ponds. Here the supply of natural food will be somewhat greater but still almost negligible compared with the requirements of growing fish, owing to the density of the fish in the ponds.

It is obvious that some form of selection of parents could be exercised in the field at the time of stripping, provided a limit were placed on the number of ova required to be collected. No such limit has been fixed in the past, the aim having been to collect as many ova as possible. In order to discover if there were any difference in the growth rate of the progeny of selected parents as compared with those of the average as represented by the customary methods of stripping, experiments were carried out on both brown and rainbow trout.

(a) *Brown Trout*

In June 1948 two pairs of fish, selected for their large size and good shape, colour, and condition were used as the test fish and a random sample of ova taken by the normal method was used as a control. The fish were stripped and the ova fertilized in the usual way, except that the resulting embryos were kept apart for transport and rearing. Subsequent treatment was the same for all, and the food and other conditions were the same as those normally used.

The first pair (A) comprised a 63·5 cm female, weighing 3290 g ($K = 1{\cdot}29$) and a 62·0 cm male weighing 2610 g ($K = 1.10$); the female yielded approximately 4850 eggs weighing 510 g (8 per cent. of her weight); the eggs were of even size and average diameter 5·92 mm.

The second pair (B) comprised a 50·5 cm female weighing 1815 g ($K = 1{\cdot}40$) and a 55·5 cm male weighing 2270 g ($K = 1{\cdot}33$); approximately 3680 eggs were obtained, weighing 255 g at stripping (5 per cent. of her weight); the eggs were of even size with an average diameter of 5.25 mm.

The sample of ova used as a control (C) comprised about 3890. They were of mixed sizes, and in a sample of 106 measured, 9, 60, and 37 had mean diameters of 4·62, 5·07, and 5·51 mm respectively; the mean for the sample was 5·18 mm.

Samples of approximately 100 from each set were preserved as ova, at hatching, and thereafter at about 2-monthly intervals until June 1949 after which data were obtained from the live fish. Set B was discontinued in April 1949 as there were insufficient survivors, a big loss being due to a faulty screen. Until December 1948 the fry were held in the hatchery troughs but at the end of that month A and C were transferred to outside ponds; no space was available for B. The survivors of these fish were raised to maturity.

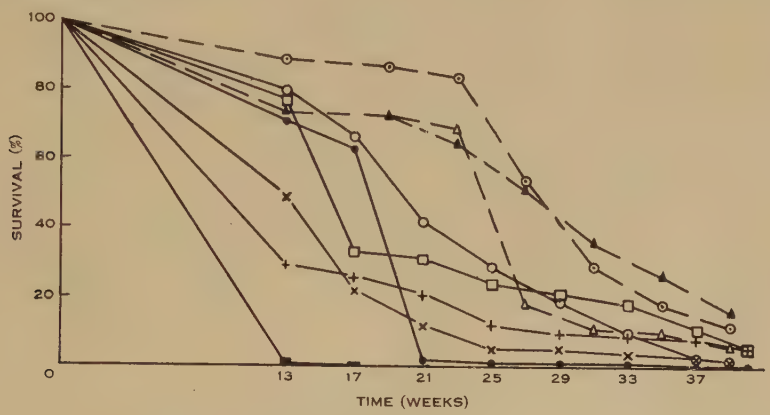

Fig. 3.—Survival of hatchery-reared brown trout. An average period of 13 weeks has been allowed for hatching. The broken lines indicate values for 1948: ○ A; △ B; ▲ C. The continuous lines represent values for 1951; progeny of C fish: ● I; + II; □ III; progeny of A fish: ○ IV; × V; ■ VI. For explanation see text.

Although there were slight differences in the growth rates of the three sets of fish during the first year after hatching they were not mathematically significant. The mortality rates for these fish during the 40 weeks following the stripping are shown in Figure 3.

In June 1951 when the survivors were 3 years of age and mature, three pairs each from A and C were selected for stripping. At that time they averaged about 38 cm in length. The best female, a C fish, 36·5 cm, weighed 620 g ($K = 1{\cdot}28$) and yielded almost 1600 ova; the other two females from C, somewhat smaller and in slightly lower condition, yielded 540 and 370 ova. The mean diameter of all ova was 4·44 mm and they were of even size.

Of the A fish suitable for stripping the three females were close to 32 cm, weighed 350 to 400 g ($K = 1{\cdot}12$–$1{\cdot}16$), and yielded 650, 480, and 420 ova of even size with a mean diameter of 4·65 mm. The subsequent fate of these progeny is dealt with below, where the detailed growth of individuals is shown (Section VI). The mortality of the offspring of these fish was surprisingly high, as shown in Figure 3. There was a large proportion of infertility, up to 100 per cent. in one pair from A. It was a C fish which produced the largest number of ova but the fry suffered a much heavier mortality than those from other pairs. The lowest infertility and lowest post-hatching mortality occurred in the A fish with the smallest number of ova.

An interesting fact shown in Figure 3 is that the survival of fish hatched in 1951 was in general at a lower level than that of their parents hatched in 1948 from natural stock. The temperature in both seasons rose gradually from 40 to 61°F during the course of the experiment.

Thus, although the offspring of the A fish were better at the beginning there was little to distinguish them from C fish as regards either growth or reproduction after 3 years in the hatchery.

(*b*) *Rainbow Trout*

An identical experiment to that described for the brown trout was started in October 1948 with rainbow trout.

The first pair (A) comprised a 58·0 cm female weighing 2720 g ($K = 1{\cdot}39$) and a 61·0 cm male weighing 2380 g ($K = 1{\cdot}05$). About 3820 ova were obtained weighing 355 g (13 per cent. of her weight), of even size and average diameter 5·49 mm.

The second pair (B) comprised a 59·0 cm female weighing 2720 g ($K = 1{\cdot}33$) and a 46·0 cm male weighing 1250 g ($K = 1{\cdot}28$); the number of ova was about 5900 and weighed 470 g (17 per cent. of her weight), of even size averaging 5·03 mm in diameter.

The control sample of ova (C) numbered about 5480 and had an average diameter of 5·03 mm.

Treatment of material and collection of data were on the same lines as described for the brown trout except that all fish were transferred to outside ponds on January 1, 1949. Again the differences in growth rates were not statistically significant. The A fish were consistently somewhat larger than either of the others, but the B fish were consistently slightly smaller than the control fish (C). Interest in this experiment again centres on the differential survival rates as between the progeny of the original fish in 1948 and their progeny at first stripping after 3 years in the hatchery.

The same general picture is shown (Fig. 4) but the difference is much more striking than for the brown trout. The survival in the 1948 samples was relatively high but that of their progeny taken in 1951 was remarkably poor. Only five pairs of fish could be stripped in 1951, there being insufficient suitable fish in the B set to provide more than one pair. The temperatures were very similar in both seasons and rose gradually from about 45 to 61°F during the time covered.

It would seem from the above that rainbow trout are more difficult to rear under hatchery conditions than are brown. There is little doubt that they are more susceptible to nutritional disorders and that they require a higher standard of food. It has frequently been noticed in the Plenty hatchery that rainbow trout retained for rearing tend to develop what is known there as the "whirling disease", the chief symptoms of which are loss of appetite, pronounced darkening in colour, and loss of equilibrium resulting in gyratory movements. Woodbury (1943) fully recounts the symptoms of a disorder due to vitamin B_1 deficiency in hatchery-reared rainbow trout which leaves little doubt that the circumstances are identical with those met with here. The disorder affects the nervous system, causing loss of equilibrium leading to progressive weakness and finally to paralysis. It is accompanied by inability to feed and pronounced darkening of the fish due to the expansion of the melanophores,

by which affected fish can be readily identified. According to this author it can be cured by injecting thiamin hydrochloride or prevented by the addition of dried brewer's yeast when the diet is low in thiamin, such as occurs when boiled or canned foods are used or when the food is dried at too high a temperature.

It is of interest to note here that the Pemberton-Warren Trout Acclimatisation Society in Western Australia (1946) experienced similar trouble with pond-reared rainbow trout, in that the ova resulting from such fish were infertile. This was overcome with complete success by feeding such fish on bran, to supplement the vitamin B, and dicalcic phosphate.

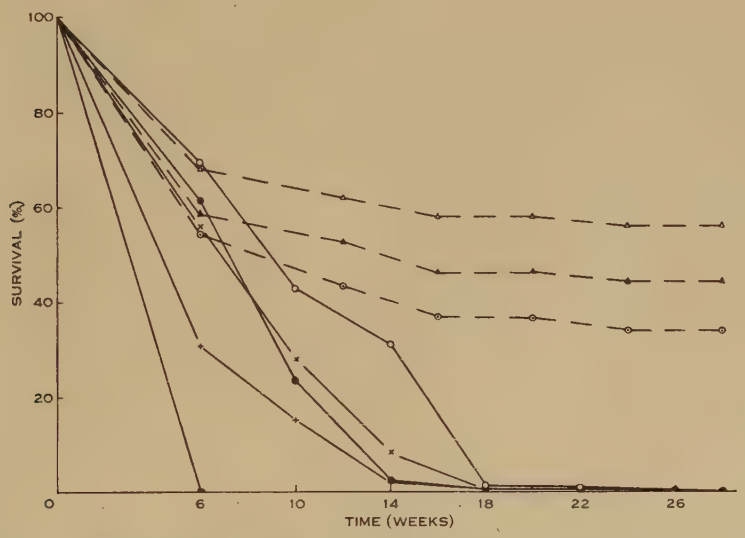

Fig. 4.—Survival of hatchery-reared rainbow trout. Hatching occurred after 6 weeks. The broken lines represent values for 1948: ⊙ A; △ B; ▲ C. The continuous lines represent values for their progeny in 1951; A fish: ■ VII; × VIII; C fish: ○ IX; ● X; B fish: + XI. At 28 weeks from fertilization survival values for VIII to XI were all 0·6 per cent. or less.

VI. Growth in Relation to Temperature

Since most of the work on the growth of fish has been carried out in the northern hemisphere it was thought advisable to follow the seasonal growth here as a direct aid to age determination. It is important to be able to fix with some certainty the time of year at which the "summer" growth recommences after the end of the period of "winter" growth.

In order to carry out this study four brown and four rainbow trout which had been hatched 5 or 6 months previously were held separately in specially constructed boxes each with its own water supply. These fish were fed daily with a slight excess of food. Water temperature records were kept throughout the period, the temperature being measured twice daily at 8.30 a.m. and 5 p.m., and for the present purposes averaged on a weekly basis. The fish were weighed and measured at approximately 4-weekly intervals and scale samples were taken.

The fish used were survivors from the experiment previously described (Section V). Numbers I and III were brown trout from the control sample, stripped in June 1951; numbers IV and V were from the A stock. Hatching took place about the middle of September. Numbers III and V died within 6 months of setting up the experiment; I survived for 18 months; IV lived for 38 months and was finally killed at an age of 3 years and 8 months from hatching, at the conclusion of the study.

Of the rainbow trout, VIII was from the A stock, IX and X were from the control sample, and XI was of B stock. These were stripped in September and hatching occurred about the middle of October. Numbers X and XI died at 6 and 12 months from the start of the study respectively. Number X showed the early symptoms of vitamin B_1 deficiency in May 1952; it was injected with 0·5 mg thiamin hydrochloride and recovered, surviving until September 1952. Numbers VIII and IX survived for 34 and 30 months respectively. Number IX was found to be carrying mature ova at 2 years of age and was stripped and fertilized with sperm from number VIII; 196 ova (average diameter 3·42 mm) were taken from this fish. These ova were infertile and all were dead within 48 hr.

Conditions in these hatchery boxes were not ideal for the growth of fish; the food was of the normal type described above and little natural food would have found its way in with the water supply. The boxes were painted black, were inside a building, and received only little indirect sunlight. The results cannot be expected to show the normal growth rate for trout, even in a hatchery, as fish held for rearing are normally placed in rearing ponds exposed to sunlight in which some natural food would grow.

The data from the regular measurements of length and weight for the three fish which survived for the longest periods (IV, VIII, and IX) are shown in Figure 5. It will be seen that for the brown trout (IV) the growth rate, which was steady but slow during the winter months, began to increase when the water temperature approached 50°F (10°C), usually at about the end of September or early in October. This was followed by rapid growth while temperatures were between 50 and 70°F. A summer check in growth occurred in January 1954, when the mean water temperature exceeded 70°F (21°C) for a fortnight during which the morning temperatures ranged from 62 to 72°F and the afternoon temperatures from 70 to 80°F. Such temperatures were not recorded in either 1953 or 1955 although afternoon readings rose to just over 70°F on a few occasions.

For simplicity the weights of the fish are not shown in Figure 5, but the K values are given from which the approximate weight in grams can be calculated by reading from the graph the corresponding length and K values for any date and substituting these in the formula $W = KL^3/100$.

The growth of the two rainbow trout was generally similar to that of the brown, but the female (IX) showed more rapid growth during its second summer though the advantage thus gained was subsequently lost.

There is a slight tendency for the condition of the brown trout to show seasonal fluctuations, rising in summer and falling in winter. This is more pronounced in the rainbows, which showed remarkable improvement in condition despite the rapid

increase in length during the summer of 1952–53, and this high condition was not lost during the following winter until after the fish were stripped (shown by the vertical line near the end of October 1953). Further loss in condition in both rainbows occurred, followed by a rapid recovery by the end of December in the male, less pronounced in the female.

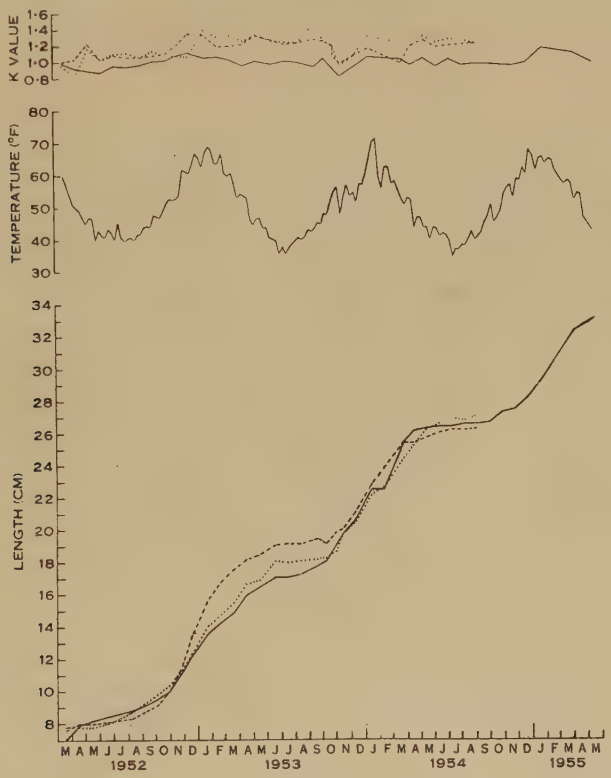

Fig. 5.—The growth of three trout in the hatchery, recorded at approximately 4-weekly intervals, together with the corresponding K values. ——— Brown trout (IV); · · · · · male rainbow trout (VIII); – – – – – female rainbow trout (IX). The mean weekly temperatures over the period are also shown.

Measurements of 486 scales taken from 111 brown trout ranging from 15·5 to 42·0 cm in length, reared at the hatchery for this experimental work, showed that the difference in size between the scales of fish from natural sources and from the hatchery (shown in Fig. 2) was maintained. The regression equation for all scale lengths for hatchery-reared fish from 3·2 to 42·0 cm is

$$Y = 0{\cdot}00501X - 0{\cdot}106,$$

which cuts the X-axis at 21·2 mm.

Statistical comparison between this equation and that for the fish from natural sources given in Section III (*d*) shows that the difference in slope is quite significant.

These regression lines meet at negative values for X (−600 mm) and Y (−3·1 mm) and thus diverge as the fish grow, indicating that if the smaller scale-size in hatchery-reared fish is real, as suggested above, it is a continuing process. If it may be accepted that for practical purposes the lines are more or less parallel over the size range involved here, then statistical comparison shows a very highly significant value for the distance separating the two lines in this range.

VII. Acknowledgments

The investigation which is covered by the series of papers of which this is the first, could not have been carried out without the cooperation of the Salmon and Freshwater Fisheries Commissioners and their staff. The assistance rendered by this body through their Chairmen (the late Mr. O. H. Hedberg until 1953, Mr. G. C. Cramp in 1953–54, and Mr. C. O. Holmes since 1954) is gratefully acknowledged.

I also wish to express my thanks to the Commissioners' Chief of Staff, Mr. H. V. Jones, to the anglers who have submitted returns of their catches, to Dr. A. T. James of the Division of Mathematical Statistics, C.S.I.R.O., to Mr. P. Sprent, Department of Mathematics, University of Tasmania, and to Mr. T. R. Marriott and other field and laboratory assistants of the Division of Fisheries and Oceanography, C.S.I.R.O.

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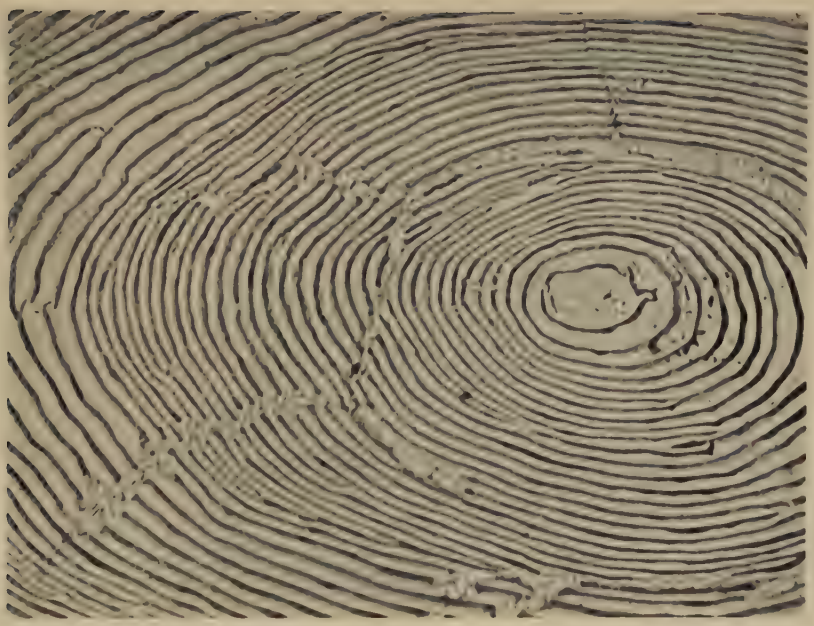

Enlarged central portion of a scale showing how the second and third circuli immediately outside the initial platelet are more widely spaced than those which follow.

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CONTINUOUS CRAYFISHING TESTS: PELSART GROUP, HOUTMAN ABROLHOS, WESTERN AUSTRALIA, 1953

By R. W. George*

[*Manuscript received May* 27, 1957]

Summary

The continuous crayfishing test at the Pelsart Group, Houtman Abrolhos, conducted in 1948, was repeated in 1953.

The numbers of crayfish available within the tested area had been reduced from 90 per haul in 1948 to 37 per haul in 1953. There was also a decrease in the commercial catch in 1953 as compared with that of 1948 in the proportion of 90 to 72; and in the catch per man in the proportion 90 to 66. The ratio of the commercial catch in 1950 (the year of maximum production and one of high fishing intensity) to that of 1953 was 90 to 34.

In 1953, there were relatively fewer very small and very large crayfish than in 1948.

The effects of the 4 years of intensive fishing between 1948 and 1953 on the composition and the numbers of crayfish available at the Pelsart Group are discussed.

The period of the test from March 15 to August 26 was divided into three catch phases, characterized by changes in the catch rates.

Except for three long-distance movements of tagged crayfish, movements were limited to a distance of approximately 2 miles.

Mating commenced on July 1 and by the end of August the majority of mature females were mated. Spawning commenced on August 22. Few females below a carapace length of 2·9 in. were mated.

I. Introduction

This paper deals with some aspects of the biology and of the fishery on the Western Australian marine crayfish, *Panulirus longipes* (Milne Edwards), at Houtman Abrolhos.

Preliminary tests were made during 1947 at a number of areas within the Pelsart, or Southern, Group of Houtman Abrolhos, and an area on the Western Reef, known as the "Channel", was selected for a continuous crayfishing test in 1948 (Sheard 1954, Fig. 2). This test was repeated in 1953. Prior to 1948, the fishery at the Pelsart Group was so limited that the data obtained in 1948 may be regarded as being drawn from an unexploited population.

The effect of 4 years' intensive fishing in this area may be estimated by comparing the results of the 1948 and 1953 tests. The following summary applies to some aspects of the biology of *P. longipes* at the Pelsart Group.

Crayfish of this species are nocturnal feeders and remain protected in reef shelters during the daylight hours. While foraging, the crayfish appear to wander at random. They have no particular locality preference for this purpose as they have been observed feeding on either sand bottom, reef faces, or reef flats.

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Females moult in May and June and mating begins in July, the females acquiring from the male a black sperm packet on the sternum. After a period of maturation of the eggs within the ovary lasting for 2–3 months, spawning occurs. According to Sheard (1954), the ripe, deeply pigmented eggs are not released immediately but adhere to the abdominal pleopods for a further period of approximately 3 months. "After hatching, the larvae spend a period estimated at about 5 months as plankton organisms in the open sea, returning to coastal waters transported by onshore current sets. They then settle on the bottom as juvenile crayfish of the same general form as the adult."

II. Continuous Test Methods

The test area lay on the Western Reef of the Pelsart Group, south-west of Number Five and Number Six Is.

Within this area, known as the Channel, this Laboratory conducted two tests, one in 1948 and the other in 1953; during those 2 years the State Fisheries Department closed this area to all commercial fishing. The present test commenced on March 15 and terminated on August 26 to conform to the period of the test in 1948.

Ten pots of the standard cane design were used in this area of approximately $2\frac{1}{2}$ acres, and the pots were emptied, rebaited, and reset in the same place as frequently as weather permitted. The crayfish taken in the pots were sexed, the presence or absence of sperm packets noted, and the carapace length measured in units of 0·1 in. The lengths of crayfish referred to in this paper are those of the carapace only. The carapace length as understood in Western Australia is the length measurement from the rear end of the horns to the end of the carapace.

Before release, all crayfish were marked by punching a distinctively shaped hole in either the telson or the exopod of the right or left uropod (the tail fan). Each month, the particular portion of the tail fan punched or the type of mark used was altered so that on recapture the time lapse between release and recapture, and the distance travelled, could be ascertained.

As in the test of 1948, all crayfish caught were removed from the test area and released at a suitable site, approximately $1\frac{1}{2}$ miles north of the test ground. The mortality during transport was nil.

III. General Catch Pattern, 1953

The catch pattern during the 1953 test for males and females is shown in Figure 1. There was a high catch rate for both sexes from March 15, at the beginning of the test, until the middle of April (haul 20). This was followed in the females by a decreased rate until the beginning of July, and a further increase (although not as high as that in the early period of the test) until the completion of the test at the end of August. The catch rate of the males after haul 20 decreased and remained reasonably steady until the completion of the test.

Correlated with the change in the rate of catch which occurred on July 1 in both tests was the first appearance of mated females in the pots. There are, however, no known biological changes which occur at the same time as the catch

rate changes in mid April, and this second arbitrary delineation is based on the change in the catch rate alone. The test period then can be subdivided into three catch phases which are termed for convenience phases I, II, and III (Fig. 1).

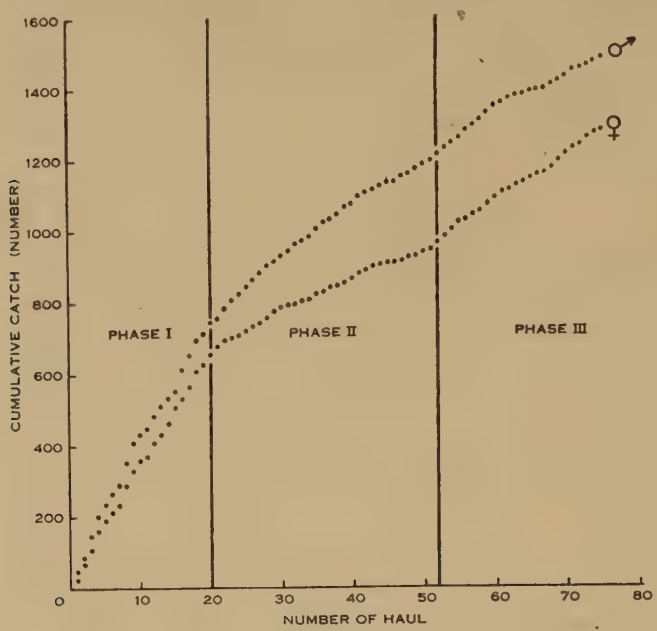

Fig. 1.—1953 Test: catch of males and females.

IV. Comparison of 1948 and 1953 Tests

(*a*) *Similarities*

The general catch pattern of the 1953 test, as outlined above, was also found in the test of 1948 (Fig. 2), there being a fairly high catch rate initially, followed by a decreased but steady catch of both sexes with a slight increase in the catch of females after July 1. The calendar dates separating the three catch phases, as indicated by the times of the changes in the catch rate and the times at which mating was first noticed, were found to differ in the two tests by only a few days in each case.

(*b*) *Differences*

The total number of crayfish of all sizes taken in 1948 with 56 hauls was 5040. In 1953, however, the pots were pulled 75 times and a total of 2755 crayfish was caught. Table 1 shows the catch number per haul for males and females separately, and for males and females combined.

In 1948, the "productivity" of the Channel was estimated by Sheard (1954) at 369. This figure represented the number of legal-sized crayfish taken per acre in the first eight hauls of the test, using 10 pots and assuming these pots to fish an area of $2\frac{1}{2}$ acres effectively. In 1953, the productivity of the Channel was 168. These values and those of Table 1 are indicative of the number of crayfish which

had accumulated on the Western Reef during two previous periods of closure, and thus give a quantitative estimation of the populations available for commercial exploitation at the beginning of the 1948 and the 1953 fishing seasons.

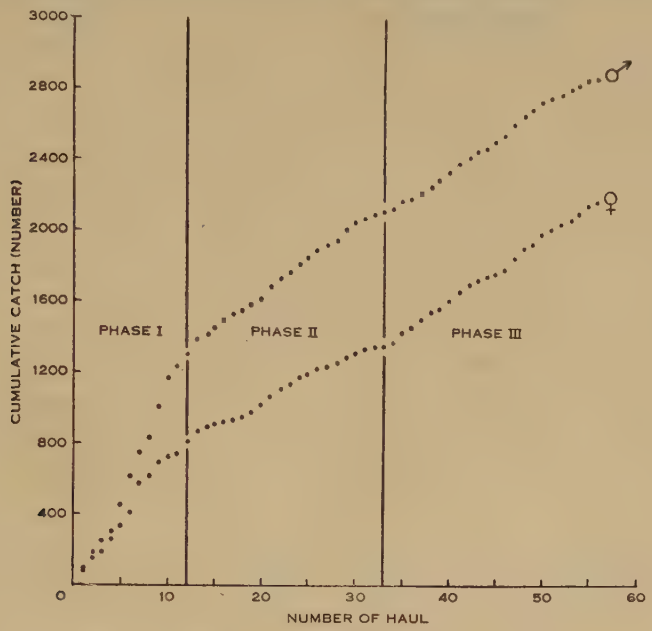

Fig. 2.—1948 Test: catch of males and females.

An assessment of changes which occurred in the population structure during the 4 years intervening between the two tests can be made by comparing the carapace length frequencies of the whole samples of the two tests (Figs. 3, 4).

TABLE 1

TOTAL NUMBERS OF CRAYFISH AND MEAN NUMBERS PER HAUL TAKEN: CONTINUOUS FISHING TESTS OF 1948 AND 1953 AT ABROLHOS

Sex	1948		1953	
	Number	Catch per Haul	Number	Catch per Haul
Male	2878	51·4	1478	19·7
Female	2162	38·6	1277	17·0
Male and female	5040	90·0	2755	36·7

(i) *Males* (Fig. 3).—In 1953, the percentages of males below 2·7 in. and above 3·5 in. were lower than the percentages of those sizes in the 1948 test. There was in 1953 a corresponding increase in the percentage of males between 2·7 and 3·5 in. as compared with that in 1948.

(ii) *Females* (Fig. 4).—A decrease in the percentage of females below 2·6 in. occurred in 1953 as compared with 1948, but little change in the percentage of the larger females (those above 3·2 in.) occurred. The increased percentage of the 2·6–3·2 in. group in 1953 is clearly illustrated.

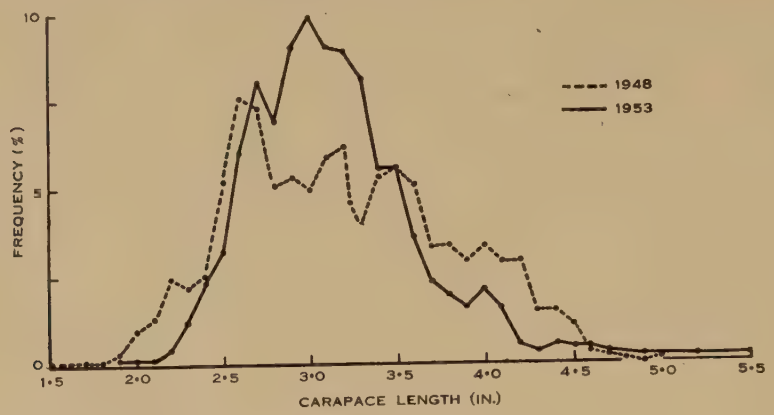

Fig. 3.—Length frequencies of male crayfish taken in 1948 and 1953 tests.

The progress numbers of males and females taken in 1948 and 1953, separated into ½-in. carapace length intervals, are graphed against haul numbers in Figures 5

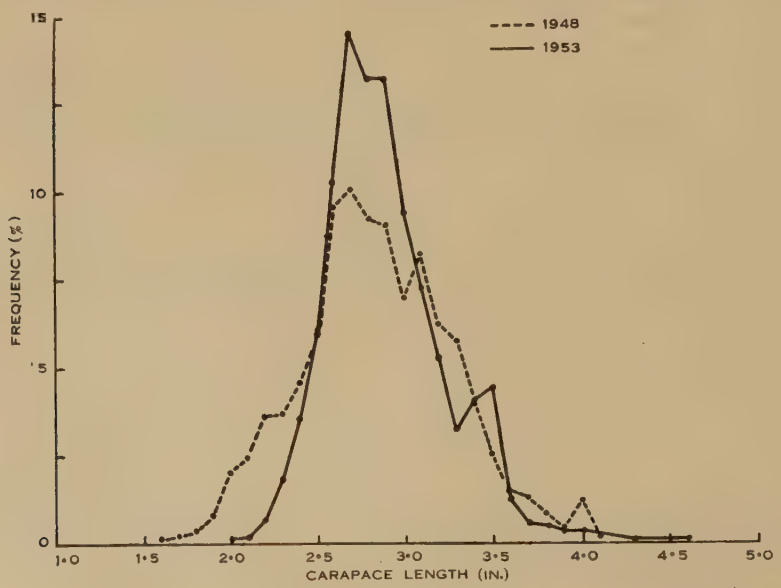

Fig. 4—Length frequencies of female crayfish taken in 1948 and 1953 tests.

and 6. This facilitates a comparison of the population structures existing throughout any one test and also allows of direct comparison between the same catch phase in the two tests.

(iii) *Males* (Fig. 5; five ½-in. groups from 2·0 to 4·4 in.).—In catch phases II and III, there was in both the tests a steady but somewhat minor catch of males as compared with that in catch phase I. There was a similar relative catch rate in 1948 and 1953 of the 2·5–2·9, 3·0–3·4, and 3·5–3·9 in. groups; but whereas in 1948 more males in the 2·5–2·9 in. group were taken than in the 3·0–3·4 in. group, in 1953 the 3·0–3·4 in. group exceeded in numbers the 2·5–2·9 in. group. The relative catch rates of the 2·0–2·4 and the 4·0–4·4 in. groups in the two tests were similar and were lower than those of the other three groups.

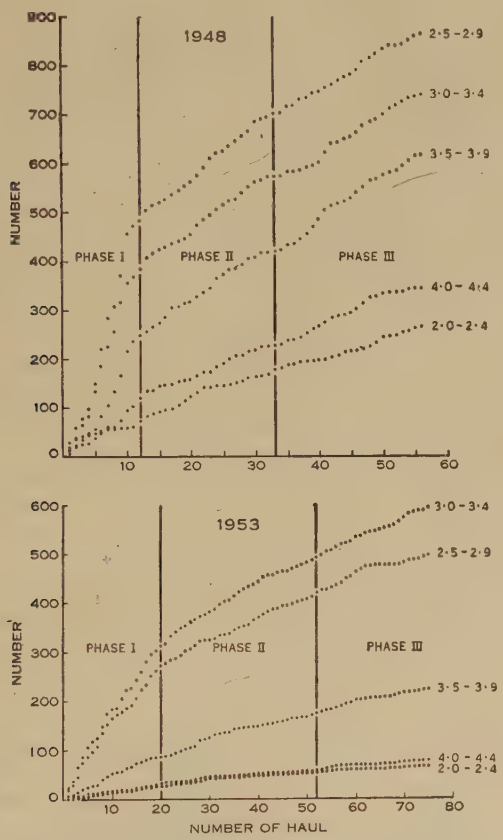

Fig. 5.—Comparison of numbers in specified size groups of male crayfish taken in 1948 and 1953 tests.

(iv) *Females* (Fig. 6; four ½-in. groups from 2·0 to 3·9 in.).—There was in 1948 a relative increase in the rate of catch during catch phase III of the three larger groups (2·5–2·9, 3·0–3·4, and 3·5–3·9 in.), and a steady catch of the small 2·0–2·4 in. group throughout the whole test period. In 1953, only the two larger groups (3·0–3·4 and 3·5–3·9 in.) showed the increased catch rate following catch phase II. In contrast to the increased catch of the 2·5–2·9 in. group during catch phase III in 1948, this group of females in 1953 was caught at a steady rate throughout

catch phases II and III. The 2·0–2·4 in. group in 1953 showed a steady low catch rate during the three catch phases.

In 1953, there was a proportionate increase in the catch of the 2·5–2·9 in. group compared with that of 1948. Whereas in 1948, catches of all other groups approximately doubled those of 1953 at the end of catch phase II, the number of females of the 2·5–2·9 in. group caught at that time was the same in the two tests.

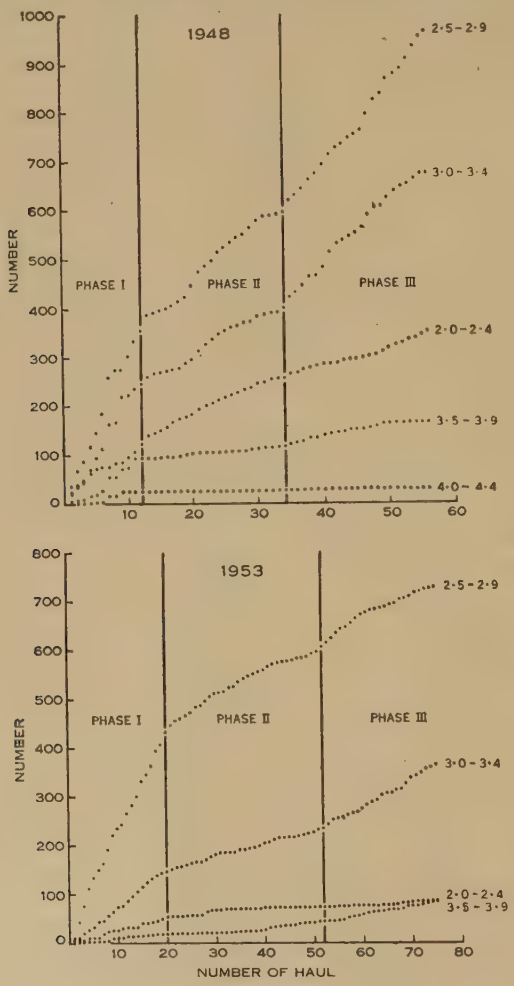

Fig. 6.—Comparison of numbers in specified size groups of female crayfish taken in 1948 and 1953 tests.

The mean carapace length, the standard deviation, and the standard error of males and females in the two tests are given in Table 2. Comparing the mean carapace lengths of the crayfish, using the t-test there was in 1953 a significant increase in the carapace length of the females and a significant decrease in that of the males. In each test, the females were smaller than the males and their size range more limited. The percentage of males in the total catch of 1948 was 57 and in 1953, 52.

V. Tagging Results

The punch marks on the tail fan of several recaptured crayfish were indistinct and only those which were clearly defined are recorded. Table 3 gives the relevant

Table 2

STATISTICS OF CARAPACE LENGTH FREQUENCIES

Data	Male		Female	
	1948	1953	1948	1953
Mean (in.)	3·185	3·130	2·837	2·893
Standard deviation	0·616	0·480	0·436	0·340
Standard error	0·0115	0·0125	0·0094	0·0095
t-test for difference between means	$t = 3·00$ $0·01 > P > 0·001$		$t = 3·97$ $P < 0·001$	

Table 3

TAGGING RESULTS OF CRAYS RELEASED, GUN I., 1953

Month Released	Place of Recapture	Date of Recapture	Movement		
			Direction	Distance	Time (months)
March	Channel	20.iv.53	South	2 miles	1
March	Gun I.	24.iv.53	Nil	Nil	1
March	Gun I.	24.iv.53	Nil	Nil	1
March	Channel	1.vii.53	South	2 miles	2½
March	Gun I.	—.iv.54	Nil	Nil	13
March	Gun I.	—.iv.54	Nil	Nil	13
April	Gun I.	20.iv.53	Nil	Nil	1
April	Channel	21.v.53	South	2 miles	1
April	Stick Is.	21.v.53	East	2 miles	1
April	Gun I.	—.iii.54	Nil	Nil	11
April	Gun I.	—.iii.54	Nil	Nil	11
April	Gun I.	—.iv.54	Nil	Nil	12
April	Gun I.	7.v.54	Nil	Nil	13
June	Wallabi Is.	25.vii.53	North	35 miles	1½
June	Geraldton	24.x.53	East	30 miles	4
July	Gun I.	—.iv.54	Nil	Nil	9
July	Geraldton	3.ii.54	East	30 miles	7
July	Gun I.	20.v.54	Nil	Nil	10
July	Gun I.	20.v.54	Nil	Nil	10
August	Gun I.	—.iv.54	Nil	Nil	8

data on the movements of these crayfish. Details of the size and the sex of the recaptured crayfish are incomplete, as the crayfish were partially processed before

they were recognized by factory workers or Fishery Inspectors. Only three crayfish of the 20 reported were recaptured more than 2 miles distant from the release area. Two of these moved 30 miles eastwards to Geraldton in 4 and 7 months respectively. The third crayfish was recaptured at the Wallabi Group, 35 miles north of the release area, after a period of only 6 weeks.

Sheard (1949, Fig. 1) obtained a similar movement in a northerly direction of crayfish released in several areas within the Pelsart Group in 1947 and 1948; two were recaptured at the Easter Group and another at the Wallabi Group. No recoveries from the Geraldton waters, east of the release area, were reported during those tests.

The remaining 17 tagged crayfish which were recaptured in 1953 and 1954 had moved over short distances, or were recovered in the same area in which they were released, even after a time lapse of 13 months. Three of these crayfish were recaptured within the test area. Many small local movements of crayfish within the Pelsart Group were also recorded in 1947 and 1948.

VI. Deep-water Test

A single haul of four pots was made in 23 fm on April 26, 3 miles west of the Western Reef opposite the Channel test area. The captured crayfish were measured, and marked distinctively to investigate the possibility of a movement of these deep-water crayfish over the Western Reef into the island shallows. The 60 captured crayfish were marked and released at that site, but none were recovered during subsequent fishing operations on the inner side of the Western Reef.

The ratio of males to females in this haul was 52 : 48, and the range over which the male and female carapace lengths were distributed was more limited than that of the main test conducted on the shallows. In the deep-water test, the males ranged in carapace length from 2·5 to 4·0 in. and the females from 2·6 to 3·4 in. Only 5 per cent. of the catch were under size. The colour of the crayfish, in contrast to the lighter-coloured shallow-water crayfish, was dark red, typical of those crayfish found in the deeper waters surrounding the island group.

VII. Mating and Spawning Observations

The appearance of sperm packets or "tar spots" was first noted on July 1. Almost day-to-day increases in the numbers of mated females were observed after this date; the percentage of mated females in July and August is sufficient to show this trend: 45 per cent. in July, 63 per cent. in August, and for the last four hauls made in August 82 per cent.

Of the females smaller than 2·9 in. in carapace length caught in July and August, only a few possessed sperm packets (Fig. 7), and the majority of females above 3·1 in. had been mated by the end of August.

Sutcliffe (1951), working on the Bermuda spiny lobster, *Panulirus argus*, uses as his criterion for maturity the presence of eggs on the abdomen and states that "sexual maturity of the females is attained some time after the carapace length reaches about 90 mm". He then refers to all females above this carapace length as mature, regardless of their position in the breeding cycle.

The limited number of spawned crayfish taken during the period of the present test makes the use of Sutcliffe's criterion for maturity unsuitable in this case. Instead, mature females are regarded here as those which possess sperm packets and show some signs of egg development within the ovary. A certain degree of gonad activity, not necessarily accompanied by discrete egg development, is presumed to be a prerequisite for the successful conclusion of the mating behaviour pattern. This

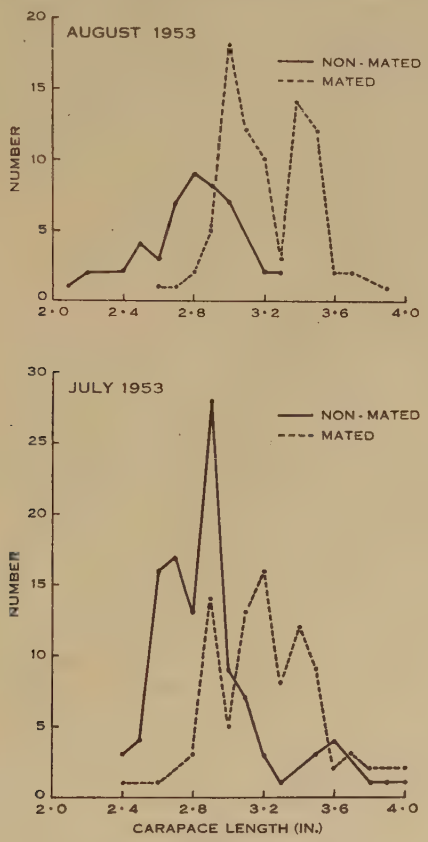

Fig. 7.—Length of non-mated and mated females in July and August 1953.

could explain the fact that in *P. longipes* some of the smaller females possessing sperm packets show no signs of external eggs, even in the height of the spawning season. This condition has been found to exist also in *P. argus* in Bermudan waters (Sutcliffe 1951).

During the 1953 test, only four berried females were recorded, on August 22 (two), August 24, and August 26, measuring respectively 3·4, 3·5, 3·5, and 2·7 in. In each case the surface of the sperm packet was eroded and the cavities in which the sperm had resided were clearly visible. The limited observations on mating and spawning made in 1948 are in agreement with the results of the 1953 investigation in the appearance of sperm packets early in July and of berried females on August 22.

VIII. Discussion

The methods of sampling the populations in the Channel test area in 1948 and 1953 were similar, so that comparison of the results obtained in these two tests is possible. At the same time inferences as to the actual density and movements of the population as a whole must be made with some reservations.

(a) *Factors Influencing the Rate of Catch during Fishing Tests*

The number of crayfish caught at each haul in the 10 baited pots used in the test area was not constant throughout the test period, and the rate of catch in any one period during the test may have been determined by the interaction of a number of factors, including the following:

(i) The number of crayfish available within the test area as a result of an accumulation during the close season;

(ii) The number of crayfish moving into and out of the test area during the period of the test;

(iii) Moult condition, influencing reactions of crayfish to baited craypots;

(iv) The availability of the natural food of crayfish;

(v) Movements and activity of predators.

(i) *Accumulated Stock.*—The fact that there are more crayfish caught by each fisherman at the beginning of a fishing season than at the close of the previous season indicates that there is recruitment of crayfish into the general fishing areas during the intervening period of closure. The gradual reduction of the commercial catches and of the catches within the test area in the *early* part of a season is mainly a result of the continued removal of crayfish from this accumulation.

It is suggested that the majority of the crayfish taken throughout catch phases I and II are drawn from this general accumulation, and that the catches during catch phase III are more dependent on the heightened post-mating activity of the females.

(ii) *Random Wanderings and Directed Migration.*—In 1948, more than 5000 crayfish were caught within the test area of only 2½ acres. It is unlikely that this number of crayfish could be drawn entirely from a more or less sedentary stock which had accumulated within the test area alone prior to the opening of the fishing season. It is suggested (Sheard 1954) that there is some continual replacement of crayfish caught within the test area by others moving in from adjacent reef areas. This interchange occurs at night when the crayfish are randomly wandering over the reefs in search of food. They may or may not return to their previous shelter after feeding, but during the day-time they do remain relatively quiescent in the shelter selected.

The continuous tests were designed to indicate changes in the availability within one area on the reef rather than the degree of interchange between adjacent reef areas.

(iii) *Moult Condition and Crayfish Activity.*—Inferences drawn from samples of crayfish caught in craypots which are in effect fixed to the bottom during their trapping period, and which depend on the type of activity of individual crayfish

within the range of the pots, differ considerably from those resulting from trawling and netting operations in teleost fisheries. In such cases where moving nets are passed through aggregations of fish a more direct estimate of population density may be obtained. The entry of crayfish into craypots is motivated primarily by the comparative attractiveness of the bait against that of their natural food; thus the samples consist mainly of actively searching crayfish. Recently moulted crayfish are rarely captured, as moulting animals are generally inactive and physically weak, preferring to remain in protected reef pockets until some hardening of the shell has begun. These crayfish when captured in craypots are referred to as "newly moulted" (Sheard 1949, 1954) and possess an exoskeleton in Stage V of Von Bonde's moulting classification (Von Bonde and Marchand 1935), i.e. "hardening new shell (shell 'gives' considerably at sides when squeezed, but is strong enough to withstand handling)". Since *Jasus lalandii* (Milne Edwards) are captured in pots in Stage IV ("soft new shell—shell of consistency of thin membrane"), it would appear that that species in South Africa actively seeks food earlier in terms of Von Bonde's moult classification than does *P. longipes*.

Travis (1954) reported feeding 5–7 days after moulting in *Panulirus argus*, (Latreille) while Lindberg (1952) recorded normal feeding activities in *Panulirus interruptus* (Randall) after 6–8 days. The relative increase in the number of females caught during catch phase III is indicative of a return to or of an increase in their normal feeding behaviour after moulting in June.

(iv) *Natural Food.*—Crayfish are scavengers. Examinations of stomach contents reveal the presence of coral fragments, seaweeds, fish remains, Foraminifera, shell fragments, and sand. The stomachs of crayfish caught by hand were examined, since the stomach contents of animals trapped in craypots consist mainly of the particular type of bait used in the craypot.

It is not unreasonable to assume that there are seasonal variations in the availability of the natural foods of crayfish. Evidence such as the periodic spawning and growth of some corals (Marshall and Stephenson 1933), the periodic occurrence of some pennate diatoms (Marshall 1933, Fig. 1), and the seasonal growth of seaweeds support this assumption.

These and other occurrences could influence the catches of crayfish throughout the test period as the bait (the type was not varied throughout the test) is dependent for its relative powers of attraction on the availability of these natural foods, i.e. a direct competition exists between the two.

(v) *Crayfish Predators.*—The influence of crayfish predators cannot be overlooked when considering the numbers of crayfish available for trapping in a particular area. Stomach contents of a number of fish—the Westralian jewfish (*Glaucosoma hebraicum* (Richardson)), the snapper (*Chrysophrys unicolor* (Quoy & Gaimard)), the North-west snapper (*Lethrinus fletus* (Whitley)), small reef fish, notably the Abrolhos groper (*Choerodon cyanodus* (Richardson)), and various ground sharks often contain crayfish of various sizes.

Octopus spp. have frequently been found in craypots, together with partially consumed crayfish, which suggests that in the wild they also can be regarded as natural predators of adult crayfish. Other animals which are plankton feeders reduce

the number of crayfish larvae, thereby influencing the future availability of crayfish in a given area.

The actual reduction in numbers of crayfish both by the predators of the adult crayfish and by those attacking the larval forms has not been estimated. However, variations in the food requirements as well as in the number of predators on the adult crayfish will be reflected to some extent in the catches of crayfish during a fishing season.

(*b*) *Comparison of Results*: 1948, 1953

It is evident from Figures 1 and 2 that the relative changes in catch rates throughout the two test periods were similar, even though the total number of crayfish caught in the 1948 test was almost double that caught in 1953. It is suggested here that at least the same five factors influence the catches during the two test periods, and these operate more or less independently of the total number of crayfish available at the beginning of the test periods.

TABLE 4

ANNUAL COMMERCIAL CATCH OF CRAYFISH, PELSART GROUP

Annual catches in 1000-lb units

1947	1948	1949	1950	1951	1952	1953
322·1	432·1	750·4	788·3	502·2	395	294

During catch phases I and II, crayfish were mainly drawn from the relatively large stock which had accumulated within and surrounding the test area before the commencement of the tests. The numbers of crayfish in this accumulated stock were gradually reduced until other factors became equally important in determining the availability. It is in catch phase III that the factors discussed in Section VIII (*a*) (iii) became important, resulting in relatively higher catches of mated females.

The number of crayfish taken during the 1953 test was lower than the number taken in the test of 1948 (Table 1). The fact that there is also a reduction in the commercial catch of 1953 compared with that of 1948 suggests that there has been a real reduction in the abundance of crayfish over the entire Pelsart fishing grounds and not only a reduction in the numbers of crayfish available within the restricted test area.

When compared with the highest commercial catch of 788,300 lb in 1950, the catch of only 432,100 lb in 1948 suggests that in this year (1948), the Pelsart grounds were not being fished to their fullest extent. After 1950, however, the commercial catches within the reef limits have declined even though the fishing intensity has remained relatively constant (see Table 4).

The ratio of the commercial catch during 1950 to that of 1953 (years of intensive fishing) was 90 to 34. During the tests of 1948 and 1953 the test area was also intensively fished, and a comparable reduction in the abundance of crayfish within

that portion of the grounds tested in those two years is shown by the catch per haul of 90·0 crayfish in 1948 and 36·7 in the 1953 test.

Since 1948, there have also been various alterations in the structure of the population within the test area. Comparing the 1953 carapace length frequency figures with those of 1948, the following alterations in the population structure are apparent: a higher percentage of females in 1953; an increase in the average length of females and a decrease in the average length of males; a relative increase in the 2·5–2·9 in. group of females in 1953; an increase in the 3·0–3·4 in. group relative to the 2·5–2·9 in. group of males in 1953 as compared with those of 1948.

These observed structural changes in the 1948 and 1953 samples may be due to a number of factors, including those which are a direct result of the removal of large quantities of crayfish from the whole Pelsart fishing grounds in the intervening years between the two tests. The total weight marketed from Pelsart in the years 1949, 1950, 1951, and 1952 was 2,436,000 lb.

The reduction in the average length of males may be due to the marketing of the slower-growing very large males. The absence of these large crayfish, which competed with the smaller crayfish for food and shelter, has facilitated the accommodation of an increased number of smaller-sized crayfish within a given area.

The lowering of the population density by commercial exploitation, thereby decreasing intraspecific competition, has resulted not only in a lowered absolute number of crayfish available, but also in a relative predominance of "medium"-sized crayfish. There still exist, however, some of the same general catch patterns in each of the carapace length groups throughout the test periods. The relative increase in the catch of mature females (those above 2·9 in. in carapace length) following the end of catch phase II, for example, is observed in both tests, as this phenomenon is a function of the biological activity of the female and is independent of the absolute numbers available.

The more or less constant catch rates of both males and females below 2·5 in. in carapace length throughout the whole test period in 1948 and 1953 is also indicative of certain factors operating which are independent of the population density. Perhaps the main reason for the steady rate of catch of these pre-mature crayfish is a result of their random feeding movements over the reefs following their lodgment as larvae. Major dispersal of crayfish is not due to any large-scale movements of the adult crayfish, but rather to the relatively passive movements of the larval stages in the surface and mid-water current systems.

Although no crayfish which had been tagged in the deeper waters to the west of the test area have been recaptured on the reef shallows, the possibility that this relatively dense population, particularly those immediately outside the reef, was responsible for some recruitment on the shallower reef areas (Sheard 1954) cannot be eliminated. An examination of the carapace length frequency of the deep-water sample (3 miles west of the main reef) indicates that it was composed of immature and recently matured animals. Some of these presumably moved into the shallows, partly as a result of the increased population pressure due to the development and growth of recently lodged larvae, and partly as a result of some directed migration of the adults following maturity.

IX. Acknowledgments

The work has been made possible through the general cooperation of many people interested in problems of the Western Australian fisheries. Among these the author wishes to thank the following for more specific assistance: Mr. A. J. Fraser, Superintendent of Fisheries, Mr. S. W. Bowler, Fisheries Inspector at Geraldton, and others of the staff of the State Department of Fisheries for their cooperation and assistance; Mr. R. Page and Mr. C. Hancock, fishermen of Geraldton, for technical assistance in the carrying out of the tests; Professor H. Waring, Department of Zoology, University of Western Australia, for laboratory accommodation and advice; and Dr. K. Sheard, Officer-in-Charge of this Laboratory, for reading and criticizing the manuscript.

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THE AUSTRALIAN PORTUNIDS (CRUSTACEA; PORTUNIDAE)

II. THE GENUS CHARYBDIS

By W. Stephenson,* Joy J. Hudson,* and B. Campbell*

[*Manuscript received January* 29, 1957]

Summary

The 12 species of *Charybdis* known from Australia, including two new records, are keyed and illustrated. First pleopods of the males are considered in greater detail than in past works, and a key based on their features is included. Minor changes in Leene's (1938) synonymy are proposed.

I. Introduction

The genus *Charybdis* de Haan, 1835, which is considered after *Thalamita* because of their close relationship (see Stephenson and Hudson 1957), has been monographed by Leene (1938). It is now given abbreviated treatment, and Leene should be referred to for a discussion of the genus and its subgenera, for citation of original literature, for extensive synonymies, for full descriptions of the general features of each species, and for keys to the Indo-Pacific species.

The present paper details and discusses the Australian species, and is based upon the collections in Australian institutions at January 1956. It makes minor amendments to Leene's synonymies, gives later references, includes keys to the Australian species which are believed to be more workable than Leene's, and also gives photographic illustrations of intact animals and male abdomens.

In the previous paper on the genus *Thalamita*, the importance of the first pleopods of the male was stressed. In *Charybdis* there is much greater uniformity in this structure than in *Thalamita*, with two consequences. Firstly, a generic description is possible; and secondly, it is necessary to give more detailed descriptions than have been attempted previously (Chopra 1935; Leene 1938).

Key to Australian Species of the Genus Charybdis, Based on General Features

1. Basal antennal joint joins front, excluding antennal flagellum from orbit (see Plate 5*B*) . . 2
   Basal antennal joint does not join front, hence antennal flagellum stands in upper portion of orbit (see Plate 5*A*) . . . . . *C.* (*Gonioneptunus*) *bimaculata*

2(1). Posterior border of carapace curved; posterodistal border of arm of cheliped not spinous (subgenus *Charybdis*) 3
   Posterior border of carapace straight; posterodistal border of arm of cheliped spinous . . . . . *C.* (*Goniohellenus*) *truncata*

3(2). Carapace with conspicuous longitudinal light mark (or cross) extending over three-quarters of its length . . . . . *C. cruciata*
   Carapace either without longitudinal mark, or if present not extending over half of its length 4

4(3). Under surface of hand with squamiform markings or regular rows of large granules 5
   Under surface of hand smooth or only microscopically granular 7

* Department of Zoology, University of Queensland, Brisbane.

5(4). Frontal lobes sharply spiniform (anterolateral teeth very sharp) ..... *C. miles*
Frontal lobes rounded 6

6(5). Last 4 anterolateral teeth sharp ..... *C. jaubertensis*
Last 4 anterolateral teeth consisting of blunt lobes ..... *C. natator*

7(4). Second anterolateral tooth much smaller than 1st 8
Second anterolateral tooth equal to or only slightly smaller than 1st 9

8(7). Carapace broad, length/breadth less than 0·6 ..... *C. anisodon*
Carapace of normal shape, length/breadth more than 0·6 ..... *C. orientalis*

9(7). Hand of cheliped swollen, with convex sides 10
Hand of cheliped massive but not swollen, with parallel sides 11

10(9). No mesobranchial ridges on carapace ..... *C. callianassa*
Two mesobranchial ridges on carapace ..... *C. variegata*

11(9). Carpus of natatory leg with a spine (seen in ventral view, Fig. 1*A*) ..... *C. helleri*
Carpus of natatory leg without a spine ..... *C. lucifera*

II. First Male Pleopods

General Features (see Figs. 2, 3*B*)

Unless otherwise stated, examinations and figures are based upon unstained and uncleared preparations of the left pleopod viewed as if *in situ* from the under surface.

Hollow, distal opening subterminal after a swollen base, distal half thinner and bent outwards. Inner surface with a lip (normally small), and with a flared membrane running in a curve from upper to outer surface. Three series of bristles in the distal half, and especially near the aperture: (1) *inner*, beginning as a band on the under surface and moving to the inside near the membrane; (2) *upper*, in the region of the membrane and extending distally beyond it; (3) *outer*, the most conspicuous of all.

In the descriptions of the pleopod under specific heads, general shape and features of the membrane are only mentioned if they are unusual, while the bristling receives attention throughout.

Key to Australian Species of the Genus Charybdis, Based on Pleopod Structure

Two species (*C. anisodon* and *C. variegata*) have not been examined and are included from the literature.

1. Lip protruding 2
Lip not protruding 3

2(1). Outer bristles below the membrane short ..... *C. jaubertensis* (Figs. 2*A*, 3*A*)
Outer bristles below the membrane long ..... *C. orientalis* (Figs. 2*B*, 3*B*)

3(1). Membrane starts near the tip 4
Membrane starts some distance from the tip 5

4(3). Some of the upper bristles relatively long ..... *C. variegata* (Fig. 3*C*)
Upper bristles either absent or all small ..... *C. callianassa* (Figs. 2*C*, 3*D*)

5(3). Some outer bristles fringed ..... *C. truncata* (Figs. 2*D*, 3*E*)
None of the outer bristles fringed 6

6(5). Upper bristles in 2 distinct rows; outer bristles opposite membrane typically long and dense 7
Upper bristles either in a distinct single row, or if more than 1 row these indistinct; outer bristles opposite membrane sparse and of moderate length 8

7(6). Outer subterminal bristles forming dense tuft ..... *C. cruciata* (Figs. 2*E*, 3*F*)
Outer subterminal bristles not forming dense tuft ..... *C. lucifera* (Figs. 2*F*, 3*G*)

8(6). Upper bristles showing long regular distinct row of up to 15 bristles ..... *C. natator* (Figs. 2*G*, 3*H*)
Upper bristles not showing long regular distinct row 9

9(8). Upper bristles extending beyond the membrane 10
Upper bristles not extending beyond the membrane 11

10(9). Upper bristles extending almost to the tip ..... *C. miles* (Figs. 2*H*, 3*I*)
Upper bristles stopping well before the tip ..... *C. helleri* (Figs. 2*I*, 3*J*)

11(9). Region beyond membrane extensive ..... *C. orientalis* (Figs. 2*B*, 3*B*)
Region beyond membrane short ..... *C. bimaculata* (Figs. 2*J*, 3*K*)

III. Australian Species: Records and Comments

These follow in alphabetical order of subgenera, and alphabetical order of species within subgenera. Dimensions are of carapace breadths; starred specimens are those illustrated.

Charybdis (Charybdis) anisodon (de Haan, 1850)

Plate 1, Fig. 1

Charybdis (*Charybdis*) *anisodon* Leene, 1938, pp. 64–7, figs. 29, 30. Buitendijk, 1947, p. 281.
Charybdis anisodon Sakai, 1939, pp. 405–6.

Material Examined

WESTERN AUSTRALIA: At Zool. Dept., Univ. Qld.: 1, sex indet., 44 mm,* Exmouth Gulf, June–Sept. 1954, otter-trawled in 5–10 fm, per Division of Fisheries and Oceanography, C.S.I.R.O. NORTHERN TERRITORY: At Aust. Mus.: ♀ 25 mm, Sir Edw. Pellew Grp., Gulf of Carpentaria, pres. Oct. 1923, Dr. W. E. J. Paradice (regd. No. P6598, dry collection).

Male Pleopod (after Leene)

Neck narrow and abruptly bent. Membrane distant from tip. Inner spines, a short stout row; upper spines, short row of spinules continued short distance under the membrane; outer spines, longer row of large spines continued to under surface as row of little spinules.

Comments

The present specimens, like the types reported on by Buitendijk (1947), have the 2nd anterolateral tooth smaller than the 1st. However, they agree more closely with Leene's (1938) description than Buitendijk's in the distinctness of the carapace ridges.

Distribution

Known from the Red Sea to New Caledonia, but not previously from Australia.

Charybdis (Charybdis) callianassa (Herbst, 1789)

Figs. 1*B–D*, 2*C*, 3*D*; Plate 1, Fig. 2; Plate 4*A*

Charybdis (*Goniosoma*) *callianassa* Chopra, 1935, pp. 489–91, fig. 11 (male pleopod), pl. IX, fig. 1.
Charybdis (*Charybdis*) *callianassa* Leene, 1938, pp. 81–4, figs. 41–43.

Material Examined

46 ♂♂ (14–61 mm); 19 ♀♀ (17–50 mm); 1, sex indet., 10 mm. *Sacculina* infection, 9 per cent.

QUEENSLAND: Gulf of Carpentaria (Normanton), Gatcombe Hd. (Facing I.), Moreton Bay (Scarborough, Woody Pt., Pat's Pt.). WESTERN AUSTRALIA: C. Bossut, Ninety Mile Beach, C. Jaubert, Wallal, Roebuck Bay. NORTHERN TERRITORY: Bathurst I.

Fig. 1.—*A*, natatory leg of *C. helleri*, showing spine (*s*) on carpus; *B*, *C. callianassa*, showing typical carpus; *C*, *D*, carapace variation of *C. callianassa* with age. *C*, 10 mm; *D*, 36 mm.

Recorded habitats.—Trawled in sandy mud and shells, 3–6 fm.

Material illustrated.—Photograph: ♂ 52 mm, 3½ miles S. Woody Pt. Pier, 26.x.52, coll. E. M. Grant (at Zool. Dept., Univ. Qld.). Male pleopods: whole mount, (1) as above, (2) ♂ 19 mm, off Roebuck Bay, Sept. 1929, A. A. Livingstone, dredged 5–9 fm (Aust. Mus. regd. No. P2635); tip, ♂ 36 mm, ESE. Scarborough Pier, 4.viii.50 (at Zool. Dept., Univ. Qld.), and ♂ 14 mm, off Gatcombe Hd. (Facing I.), July 1929, M. Ward and W. Boardman, 9–12 fm (Aust. Mus. regd. No. P12624). Carapace outlines: indet. 10 mm, off Roebuck Bay, Sept. 1929, A. A. Livingstone, dredged 5–9 fm (Aust. Mus. regd. No. P12835); ♂ 36 mm, 60 miles

within the range of the pots, differ considerably from those resulting from trawling and netting operations in teleost fisheries. In such cases where moving nets are passed through aggregations of fish a more direct estimate of population density may be obtained. The entry of crayfish into craypots is motivated primarily by the comparative attractiveness of the bait against that of their natural food; thus the samples consist mainly of actively searching crayfish. Recently moulted crayfish are rarely captured, as moulting animals are generally inactive and physically weak, preferring to remain in protected reef pockets until some hardening of the shell has begun. These crayfish when captured in craypots are referred to as "newly moulted" (Sheard 1949, 1954) and possess an exoskeleton in Stage V of Von Bonde's moulting classification (Von Bonde and Marchand 1935), i.e. "hardening new shell (shell 'gives' considerably at sides when squeezed, but is strong enough to withstand handling)". Since *Jasus lalandii* (Milne Edwards) are captured in pots in Stage IV ("soft new shell—shell of consistency of thin membrane"), it would appear that that species in South Africa actively seeks food earlier in terms of Von Bonde's moult classification than does *P. longipes*.

Travis (1954) reported feeding 5–7 days after moulting in *Panulirus argus*, (Latreille) while Lindberg (1952) recorded normal feeding activities in *Panulirus interruptus* (Randall) after 6–8 days. The relative increase in the number of females caught during catch phase III is indicative of a return to or of an increase in their normal feeding behaviour after moulting in June.

(iv) *Natural Food.*—Crayfish are scavengers. Examinations of stomach contents reveal the presence of coral fragments, seaweeds, fish remains, Foraminifera, shell fragments, and sand. The stomachs of crayfish caught by hand were examined, since the stomach contents of animals trapped in craypots consist mainly of the particular type of bait used in the craypot.

It is not unreasonable to assume that there are seasonal variations in the availability of the natural foods of crayfish. Evidence such as the periodic spawning and growth of some corals (Marshall and Stephenson 1933), the periodic occurrence of some pennate diatoms (Marshall 1933, Fig. 1), and the seasonal growth of seaweeds support this assumption.

These and other occurrences could influence the catches of crayfish throughout the test period as the bait (the type was not varied throughout the test) is dependent for its relative powers of attraction on the availability of these natural foods, i.e. a direct competition exists between the two.

(v) *Crayfish Predators.*—The influence of crayfish predators cannot be overlooked when considering the numbers of crayfish available for trapping in a particular area. Stomach contents of a number of fish—the Westralian jewfish (*Glaucosoma hebraicum* (Richardson)), the snapper (*Chrysophrys unicolor* (Quoy & Gaimard)), the North-west snapper (*Lethrinus fletus* (Whitley)), small reef fish, notably the Abrolhos groper (*Choerodon cyanodus* (Richardson)), and various ground sharks often contain crayfish of various sizes.

Octopus spp. have frequently been found in craypots, together with partially consumed crayfish, which suggests that in the wild they also can be regarded as natural predators of adult crayfish. Other animals which are plankton feeders reduce

the number of crayfish larvae, thereby influencing the future availability of crayfish in a given area.

The actual reduction in numbers of crayfish both by the predators of the adult crayfish and by those attacking the larval forms has not been estimated. However, variations in the food requirements as well as in the number of predators on the adult crayfish will be reflected to some extent in the catches of crayfish during a fishing season.

(*b*) *Comparison of Results*: 1948, 1953

It is evident from Figures 1 and 2 that the relative changes in catch rates throughout the two test periods were similar, even though the total number of crayfish caught in the 1948 test was almost double that caught in 1953. It is suggested here that at least the same five factors influence the catches during the two test periods, and these operate more or less independently of the total number of crayfish available at the beginning of the test periods.

TABLE 4

ANNUAL COMMERCIAL CATCH OF CRAYFISH, PELSART GROUP

Annual catches in 1000-lb units

1947	1948	1949	1950	1951	1952	1953
322·1	432·1	750·4	788·3	502·2	395	294

During catch phases I and II, crayfish were mainly drawn from the relatively large stock which had accumulated within and surrounding the test area before the commencement of the tests. The numbers of crayfish in this accumulated stock were gradually reduced until other factors became equally important in determining the availability. It is in catch phase III that the factors discussed in Section VIII (*a*) (iii) became important, resulting in relatively higher catches of mated females.

The number of crayfish taken during the 1953 test was lower than the number taken in the test of 1948 (Table 1). The fact that there is also a reduction in the commercial catch of 1953 compared with that of 1948 suggests that there has been a real reduction in the abundance of crayfish over the entire Pelsart fishing grounds and not only a reduction in the numbers of crayfish available within the restricted test area.

When compared with the highest commercial catch of 788,300 lb in 1950, the catch of only 432,100 lb in 1948 suggests that in this year (1948), the Pelsart grounds were not being fished to their fullest extent. After 1950, however, the commercial catches within the reef limits have declined even though the fishing intensity has remained relatively constant (see Table 4).

The ratio of the commercial catch during 1950 to that of 1953 (years of intensive fishing) was 90 to 34. During the tests of 1948 and 1953 the test area was also intensively fished, and a comparable reduction in the abundance of crayfish within

that portion of the grounds tested in those two years is shown by the catch per haul of 90·0 crayfish in 1948 and 36·7 in the 1953 test.

Since 1948, there have also been various alterations in the structure of the population within the test area. Comparing the 1953 carapace length frequency figures with those of 1948, the following alterations in the population structure are apparent: a higher percentage of females in 1953; an increase in the average length of females and a decrease in the average length of males; a relative increase in the 2·5–2·9 in. group of females in 1953; an increase in the 3·0–3·4 in. group relative to the 2·5–2·9 in. group of males in 1953 as compared with those of 1948.

These observed structural changes in the 1948 and 1953 samples may be due to a number of factors, including those which are a direct result of the removal of large quantities of crayfish from the whole Pelsart fishing grounds in the intervening years between the two tests. The total weight marketed from Pelsart in the years 1949, 1950, 1951, and 1952 was 2,436,000 lb.

The reduction in the average length of males may be due to the marketing of the slower-growing very large males. The absence of these large crayfish, which competed with the smaller crayfish for food and shelter, has facilitated the accommodation of an increased number of smaller-sized crayfish within a given area.

The lowering of the population density by commercial exploitation, thereby decreasing intraspecific competition, has resulted not only in a lowered absolute number of crayfish available, but also in a relative predominance of "medium"-sized crayfish. There still exist, however, some of the same general catch patterns in each of the carapace length groups throughout the test periods. The relative increase in the catch of mature females (those above 2·9 in. in carapace length) following the end of catch phase II, for example, is observed in both tests, as this phenomenon is a function of the biological activity of the female and is independent of the absolute numbers available.

The more or less constant catch rates of both males and females below 2·5 in. in carapace length throughout the whole test period in 1948 and 1953 is also indicative of certain factors operating which are independent of the population density. Perhaps the main reason for the steady rate of catch of these pre-mature crayfish is a result of their random feeding movements over the reefs following their lodgment as larvae. Major dispersal of crayfish is not due to any large-scale movements of the adult crayfish, but rather to the relatively passive movements of the larval stages in the surface and mid-water current systems.

Although no crayfish which had been tagged in the deeper waters to the west of the test area have been recaptured on the reef shallows, the possibility that this relatively dense population, particularly those immediately outside the reef, was responsible for some recruitment on the shallower reef areas (Sheard 1954) cannot be eliminated. An examination of the carapace length frequency of the deep-water sample (3 miles west of the main reef) indicates that it was composed of immature and recently matured animals. Some of these presumably moved into the shallows, partly as a result of the increased population pressure due to the development and growth of recently lodged larvae, and partly as a result of some directed migration of the adults following maturity.

IX. Acknowledgments

The work has been made possible through the general cooperation of many people interested in problems of the Western Australian fisheries. Among these the author wishes to thank the following for more specific assistance: Mr. A. J. Fraser, Superintendent of Fisheries, Mr. S. W. Bowler, Fisheries Inspector at Geraldton, and others of the staff of the State Department of Fisheries for their cooperation and assistance; Mr. R. Page and Mr. C. Hancock, fishermen of Geraldton, for technical assistance in the carrying out of the tests; Professor H. Waring, Department of Zoology, University of Western Australia, for laboratory accommodation and advice; and Dr. K. Sheard, Officer-in-Charge of this Laboratory, for reading and criticizing the manuscript.

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THE AUSTRALIAN PORTUNIDS (CRUSTACEA; PORTUNIDAE)

II. THE GENUS CHARYBDIS

By W. Stephenson,* Joy J. Hudson,* and B. Campbell*

[*Manuscript received January* 29, 1957]

Summary

The 12 species of *Charybdis* known from Australia, including two new records, are keyed and illustrated. First pleopods of the males are considered in greater detail than in past works, and a key based on their features is included. Minor changes in Leene's (1938) synonymy are proposed.

I. Introduction

The genus *Charybdis* de Haan, 1835, which is considered after *Thalamita* because of their close relationship (see Stephenson and Hudson 1957), has been monographed by Leene (1938). It is now given abbreviated treatment, and Leene should be referred to for a discussion of the genus and its subgenera, for citation of original literature, for extensive synonymies, for full descriptions of the general features of each species, and for keys to the Indo-Pacific species.

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Figs. 1*B–D*, 2*C*, 3*D*; Plate 1, Fig. 2; Plate 4*A*

Charybdis (*Goniosoma*) *callianassa* Chopra, 1935, pp. 489–91, fig. 11 (male pleopod), pl. IX, fig. 1.
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Fig. 1.—*A*, natatory leg of *C. helleri*, showing spine (*s*) on carpus; *B*, *C. callianassa*, showing typical carpus; *C*, *D*, carapace variation of *C. callianassa* with age. *C*, 10 mm; *D*, 36 mm.

Recorded habitats.—Trawled in sandy mud and shells, 3–6 fm.

Material illustrated.—Photograph: ♂ 52 mm, 3½ miles S. Woody Pt. Pier, 26.x.52, coll. E. M. Grant (at Zool. Dept., Univ. Qld.). Male pleopods: whole mount, (1) as above, (2) ♂ 19 mm, off Roebuck Bay, Sept. 1929, A. A. Livingstone, dredged 5–9 fm (Aust. Mus. regd. No. P2635); tip, ♂ 36 mm, ESE. Scarborough Pier, 4.viii.50 (at Zool. Dept., Univ. Qld.), and ♂ 14 mm, off Gatcombe Hd. (Facing I.), July 1929, M. Ward and W. Boardman, 9–12 fm (Aust. Mus. regd. No. P12624). Carapace outlines: indet. 10 mm, off Roebuck Bay, Sept. 1929, A. A. Livingstone, dredged 5–9 fm (Aust. Mus. regd. No. P12835); ♂ 36 mm, 60 miles

SW. C. Fourcroy, Bathurst I., 19.ix.49, G. P. Whitley, *Stanley Fowler*, submarine lamp, surface over 39 fm (Aust. Mus. regd. No. P12667).

Male Pleopod (specimens wider than *c.* 25 mm)

Bent sharply outwards somewhat behind tip, almost into a right-angled bend, such that the inner surface points forwards and the outer backwards. Membrane very near the tip. Inner spines, line of inconspicuous spinules running almost to (occasionally beyond) the membrane; upper spines, varying from none present to a single row of 4, occasionally with single bristle of a 2nd row present.

Comments

Leene's figure of the male abdomen does not show the indented distal border of the penultimate segment as in the present specimens. The length/breadth ratio of the carapace varies, owing to a decreasing length of the last anterolateral tooth with increasing size of specimen; extremes are given in Figures 1*C* and 1*D*. In small specimens the male pleopods are relatively straight (Figs. $2C_2$, $3D_2$), and in very small specimens the membrane is absent, the aperture is widely open, and the outer spines are notably developed (Fig. $3D_2$).

This species is very close to *C. variegata* (Fabr.), sharing with it the swollen hand of the chelipeds, and the only obvious difference is the absence of mesobranchial ridges in *C. callianassa*. The resemblance to *C. variegata* var. *brevispinosa* Leene, 1937 (see Leene 1938, pp. 88–90, Figs. 46, 47) is particularly close, and male pleopods of Leene's variety seem to be distinguishable only by the presence of 2 large spines on the upper surface.

Distribution

From Karachi to Darwin (Miers, fide Leene 1938) but not previously from either Western Australia or Queensland. It is common amongst penaeid prawn catches in Moreton Bay.

Charybdis (Charybdis) cruciata (Herbst, 1789)

Figs. 2*E*, 3*F*; Plate 1, Fig. 3; Plate 4*B*

Charybdis (*Goniosoma*) *cruciatus* Chopra, 1935, pp. 482–3, fig. 7 (male pleopod).
Charybdis (*Charybdis*) *cruciata* Leene, 1938, pp. 24–7, figs. 1, 2.
Charybdis cruciata Sakai, 1939, pp. 403–4, pl. LXXXII, fig. 3. Barnard, 1950, pp. 166–7, fig. 32*a*.

Material Examined

27 ♂♂ (13–158 mm); 15 ♀♀ (27–152 mm). *Sacculina* infection, 2 per cent.

QUEENSLAND: Townsville, Moreton Bay (Beechmere, Deception Bay, Scarborough, Woody Pt., Pat's Pt., Cleveland), Southport. NEW SOUTH WALES: Newcastle, Snake I. (Hawkesbury R.), Parramatta R., Botany Bay, Port Jackson, "Sydney". VICTORIA: South Beach. WESTERN AUSTRALIA: Exmouth Gulf, Fremantle, Swan R. NORTHERN TERRITORY: Sir Edw. Pellew Grp.

Recorded habitats.—Trawled 5–10 fm, sandy mud; also from live coral.

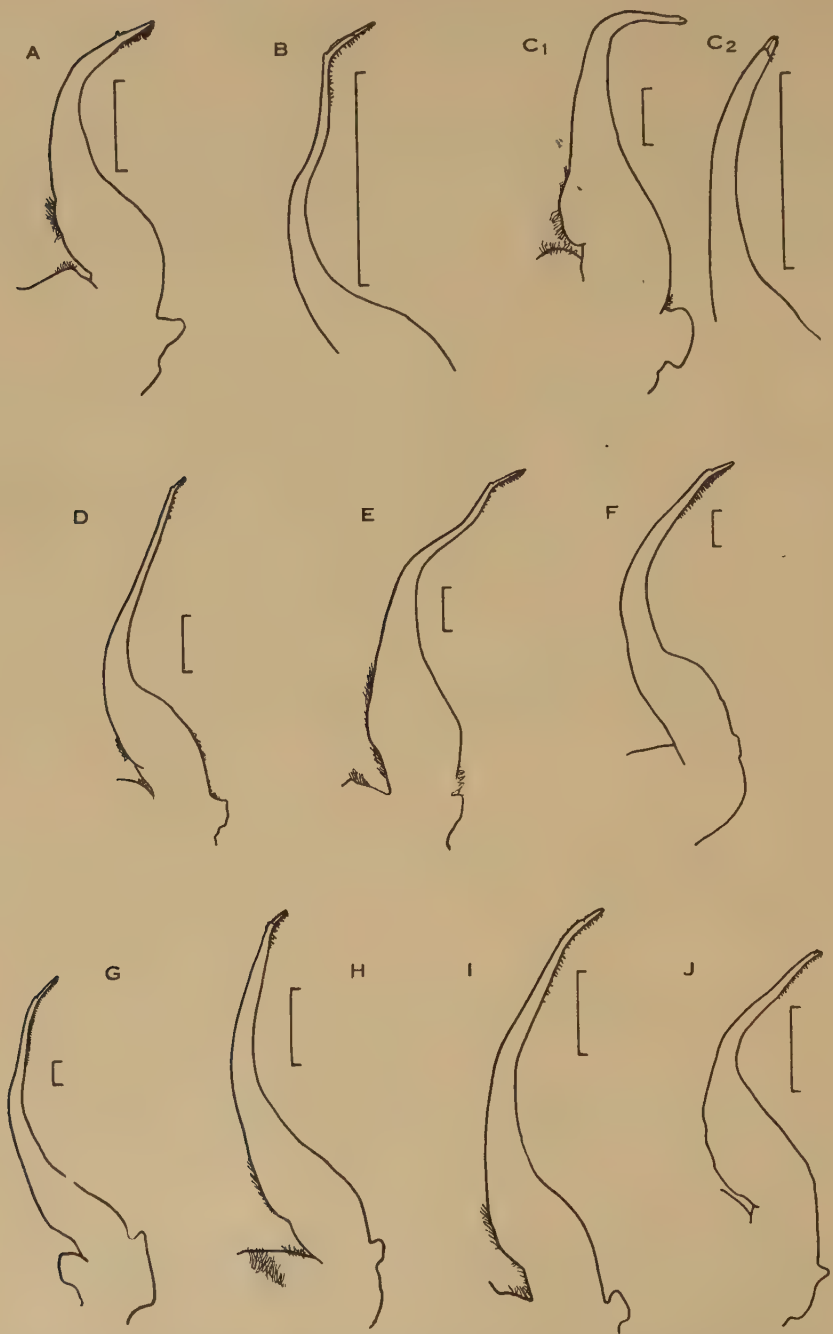

Fig. 2.—First male pleopods from stained, flattened mounts unless otherwise stated; with outer surface on right of figure. Scale lines, 2 mm. *A*, *C. jaubertensis*; *B*, *C. orientalis* (unstained); *C*, *C. callianassa*—C_1, 36 mm, C_2, 19 mm; *D*, *C. truncata*; *E*, *C. cruciata*; *F*, *C. lucifera*; *G*, *C. natator*; *H*, *C. miles*; *I*, *C. helleri*; *J*, *C. bimaculata*.

Material illustrated.—All at Zool. Dept., Univ. Qld. Photograph: ♂ 158 mm, Beechmere, via Caboolture, Nov. 1953. Male pleopod: whole mount, ♂ 78 mm, S. end Moreton Bay, 1.vi.50, coll. T. C. Marshall; tip, ♂ 72 mm, south Qld., donated, coll. unknown.

Male Pleopod

Inner spines, beginning as spinules and ending beyond the membrane as small, sparsely arranged bristles. Upper spines, 2 regular rows of fairly large bristles extending almost to tip; outer spines, beginning well back, uniformly long and dense to near tip, where bristles become shorter and more densely packed, and row passes to under surface to form a dense clump.

Comments

Pigmentation in this species is characteristic. An 18 mm ♂ in the Macleay Museum, from "Sydney", is doubtfully included in the present records. It resembles the present species in general facies but its colour is too faded to be helpful, and its antennal flagellum is not excluded from the orbital hiatus. This last would take it to the subgenus *Gonioneptunus*, but it shows no other resemblances to the described species of that subgenus.

Distribution

Ranging from India to Japan, with past Australian records from Queensland (Ward 1941), New South Wales (Haswell 1882; Ogilby 1893; Stead 1898; McNeill 1929) and eastern Australia (Henderson 1893); now from Western Australia and Northern Territory. In Moreton Bay it is common from September to February, is caught with *Portunus pelagicus*, and is highly sought after.

CHARYBDIS (CHARYBDIS) HELLERI (A. Milne Edwards, 1867)

Figs. 1*A*, 2*I*, 3*J*; Plate 1, Fig. 4; Plates 4*C*, 5*B*

Charybdis (*Goniosoma*) *merguiensis* Chopra, 1935, pp. 484–6, fig. 8 (male pleopod).
Charybdis (*Charybdis*) *hellerii* Leene, 1938, pp. 44–9, figs. 15–17. Buitendijk, 1947, p. 281.
Charybdis merguiensis Barnard, 1950, p. 168, figs. 27*d*, 32*b*.
Charybdis hellerii Edmondson, 1954, pp. 247–8, fig. 32*a–f*.

Material Examined

38 ♂♂ (12–85 mm); 34 ♀♀ (14–63 mm). Smallest ovigerous ♀ 47 mm; ovigerous ♀♀ from May, July, Dec.–Jan. *Sacculina* infection, 1·3 per cent.

QUEENSLAND: Endeavour R., Cooktown, Cairns, Port Denison, Townsville, Lindeman I., Brampton I., Cannonvale, Yeppoon, Port Curtis, Picnic I., Garden I. near Gladstone, Hervey Bay, Caloundra, Moreton Bay (Scott's Pt., Woody Pt., Wynnum), Burleigh. WESTERN AUSTRALIA: Between C. Bossut and Broome, Ninety Mile Beach. NORTHERN TERRITORY: Darwin (Middle I.), Sir Edw. Pellew Grp.

Recorded habitats.—Intertidal, under rocks and stones, among live coral, dredged 3–7 fm.

Material illustrated.—All at Zool. Dept, Univ. Qld. Photograph: ♂ 77 mm, end of N. jetty, Wynnum, 16.ix.52, coll. W.S. Male abdomen: ♂ 56 mm, S. Yeppoon,

15.i.53, coll. Zool. Dept. party. Male pleopod: whole mount, ♂ 20 mm, N. Burleigh, 23.ii.54, coll. A. B. Cribb; tip, same specimen as male abdomen.

Male Pleopod

Inner spines, relatively large, sparsely arranged, extending well beyond the membrane; upper spines, an inner row of 4–7 short spines, occasionally a single outer bristle; outer spines, beginning well back, mostly long and stout with occasional short stout bristles somewhat irregularly arranged, becoming smaller, thinner, and more crowded towards tip.

Comments

The spine on the carpus of the natatory leg is diagnostic. When alive the species can be recognized by a central lighter area of the anterior of the carapace.

Distribution

From the Mediterranean to Hawaii, with previous records from Queensland (Grant and McCulloch 1906–7) and from eastern Australia (Ward 1941), but not from Western Australia or Northern Territory.

Charybdis (Charybdis) jaubertensis Rathbun, 1924

Figs. 2*A*, 3*A*; Plate 2, Fig. 1; Plate 4*D*

Charybdis (*Charybdis*) *jaubertensis* Leene, 1938, pp. 67–8, fig. 31.

Material Examined

11 ♂♂ (9–46 mm); 14 ♀♀ (13–45 mm); 1, sex indet. (8 mm). Ovigerous ♀ 44 mm, from month of November. *Sacculina* infection, 4 per cent.

QUEENSLAND: Townsville, Scawfell I., Prudhoe I., Port Curtis, Moreton Bay (Woody Pt., Pearl Channel, Pat's Pt.). WESTERN AUSTRALIA: Roebuck Bay, Ninety Mile Beach between C. Jaubert and Wallal, between C. Bossut and Broome, Broome, Exmouth Gulf. NORTHERN TERRITORY: Peron I., Anson Bay.

Recorded habitats.—Trawled, 2–20 fm, mud and sandy mud.

Material illustrated.—All at Zool. Dept., Univ. Qld. Photograph: ♂ 46 mm, 3½ miles S. Woody Pt. Pier, 8.x.52, coll. E. M. Grant. Male pleopod: whole mount as above; tip, ♂ 42 mm, near Pat's Pt., Moreton Bay, 24.x.50, coll. T. C. Marshall.

Male Pleopod (not previously known)

Short, stout, sharply curved. Membrane inconspicuous, lip markedly protruding. Inner spines, below lip only visible from under surface, as a thin row of spinules; beyond lip, 6 or 7 are visible from above. Upper spines, single row of *c.* 9, small and thin. Outer spines, best seen from under side, beginning as a sparse, irregular band; becoming long, stout, and dense opposite membrane; then short, stout, and dense towards tip.

Comments

This species is difficult to identify from Leene's key or from Rathbun's description, because Rathbun's holotype, the only previously known specimen, is shown as having a sharp 1st anterolateral tooth. In all but the smallest of the present specimens, the 1st anterolateral tooth is broad and truncated laterally if not anteriorly.

Fig. 3.—Tips of left first male pleopods, from unstained, unflattened preparations unless otherwise stated. Scale lines, 0·5 mm. *A*, *C. jaubertensis*—A_1, upper, A_2, lower surface; *B*, *C. orientalis*, upper surface. *i.s.*, Inner spines; *u.s.*, upper spine; *o.s.*, outer spines; *m*, membrane; *l*, lip; *C*, *C. variegata* (from Leene 1938, Fig. 45) —C_1, upper, C_2, lower surface; *D*, *C. callianassa*, upper surfaces—D_1, 36 mm, D_2, 14 mm; *E*. *C. truncata*—E_1, upper, E_2, lower surface; *F*, *C. cruciata*—F_1, upper, F_2, lower surface; *G*, *C. lucifera*, stained mount, slightly twisted and flattened; *H*, *C. natator*—H_1, 100 mm, H_2, 31 mm, slightly twisted; *I*, *C. miles*, upper surface; *J*, *C. helleri*, upper surface; *K*, *C. bimaculata*, upper surface, mirror image of right pleopod.

The species is easily recognized by the male pleopods, and shares with adults of *C. callianassa* a markedly long carapace. It has also characteristic squamiform markings on the under surfaces of the chelipeds.

Distribution

Previously only known from the type locality at C. Jaubert, W. A.; now from Northern Territory and Queensland.

CHARYBDIS (CHARYBDIS) LUCIFERA (Fabricius, 1798)

Figs. 2*F*, 3*G*; Plate 2, Fig. 2; Plate 4*E*

Charybdis (*Charybdis*) *lucifera* Leene, 1938, pp. 57–60, figs. 23–25.

Material Examined

QUEENSLAND: At Zool. Dept., Univ. Qld.: ♂ 76 mm,* Mooloolabah, Nov.–Dec. 1952, coll. F. Maiden. At Aust. Mus.: ♀ 61 mm, Hope I., pres. Aug. 1913, A. R. McCulloch (regd. No. P3797). At Nat. Mus., Melb.: ♂ 67 mm, north Qld., 6.xi.80, Rev. J. E. Tenison Woods. WESTERN AUSTRALIA: At W. Aust. Mus.: ovigerous ♀ 68 mm, Bernier I. (regd. No. 4153); ♀ 54 mm, North West Cape (regd. No. 63.1955).

Male Pleopod (based on single stained specimen)

Inner spines, sparse row of small spines, probably some lost in mounting; upper spines, 2 conspicuous rows each of up to 15 long thin spines (inner row appearing short and stout in perspective view) and terminating some distance before tip; outer spines, in this specimen extremely long and stout, except near tip.

Comments

The obvious gross features of this species are the massive rounded chelipeds and the dark tips to the anterolateral teeth.

Distribution

Known from India to Japan, but not previously from Australia.

CHARYBDIS (CHARYBDIS) MILES de Haan, 1850

Figs. 2*H*, 3*I*; Plate 2, Fig. 3; Plate 4*F*

Charybdis (*Goniosoma*) *miles* Chopra, 1935, pp. 486–7, fig. 9 (male pleopod).
Charybdis (*Charybdis*) *miles* Leene, 1938, pp. 38–42, figs. 10–13.
Charybdis miles Sakai, 1939, p. 405, pl. XLVI, fig. 2.

Material Examined

5 ♂♂ (37–66 mm); 2 ♀♀ (58, 64 mm); 9, sex indet. (parts dissociated).

NEW SOUTH WALES: Newcastle, Botany Bay.

Recorded habitats.—Trawled, 21–48 fm.

Material illustrated.—All at Aust. Mus. Photograph: ♀ 64 mm, off Botany Bay, Oct. 1924, coll. M. Ward (regd. No. P7870). Male abdomen: ♂ 57 mm, Newcastle Bight, stn. 22, *Thetis* Exped., pres. March 1899, coll. E. R. Waite, 26–40 fm (regd. No. G2352). Male pleopod: whole mount, ♂ 42 mm, other data as last; tip, ♂ 66 mm, other data as last.

Male Pleopod

Only slightly curved. Deep separation between lip and membrane. Inner spines, sparse irregular row of short spines becoming longer distally and curving from under surface to appear in profile view as 4 or 5 bristles opposite membrane; upper spines, 3 rows distinguishable with difficulty, the innermost short spinules and the outer long and conspicuous; outer spines, all moderate size and approximately equally spaced except for a subterminal cluster.

Comments

Sakai (1939) notes its Japanese habitats to be at 10–50 m depth on rocky or sandy bottoms. The restriction in the known Australian distribution is presumably because the habitat has not been sampled adequately outside New South Wales. The species is easily recognized by the sharpness of the anterolateral teeth and frontal lobes, and by the slender chelipeds.

Distribution

From India to Japan, and including New South Wales (Whitelegge 1900).

CHARYBDIS (CHARYBDIS) NATATOR (Herbst, 1789)

Figs. 2*G*, 3*H*; Plate 2, Fig. 4; Plate 4*J*

Charybdis (*Charybdis*) *natator* Leene, 1938, pp. 93–7, figs. 50, 51.
Charybdis natator Sakai, 1939, p. 407. Barnard, 1950, pp. 169–70.

Material Examined

19 ♂♂ (9–145 mm); 6 ♀♀ (15–104 mm). Ovigerous ♀ 104 mm, from month of January.

QUEENSLAND: Townsville, Possession I., Albany Passage (C. York), Holbourne I. (Pt. Denison), Bowen, Mackay, Double I. Pt., Caloundra, Moreton Bay (Woody Pt., Cleveland, Myora, Pearl Banks, Peel I., Cowan Cowan), Southport. NEW SOUTH WALES: Port Jackson. LORD HOWE I. WESTERN AUSTRALIA: Exmouth Gulf, Roebuck Bay.

Recorded habitats.—At low water, in sand, mud, and weeds, also live coral; trawled 4–33 fm.

Material illustrated.—All at Zool. Dept., Univ. Qld. Photograph: ♂ 135 mm, Peel I., Apr. 1954, per Dept. Harbours and Marine. Male pleopod: whole mount, ♂ 32 mm, N. of Myora, Moreton Bay, 16.vii.39, Sci. Stud. Exped.; tip, ♂ 100 mm, Cleveland Pt., 4.xii.41, caught in crab net L.W.M., per Dept. Harbours and Marine. Juvenile: ♂ 31 mm, Stradbroke I., 16.vii.39, coll. Zool. Dept. party.

Male Pleopod (large specimens)

Long and thin distally, membrane distant from tip. Inner spines, an irregular band of short spines terminating opposite top of membrane. Upper spines, an elongate regular row, base obscured by membrane, terminating well back from tip. Outer spines, beginning as moderately long stout bristles sparsely arranged, becoming thinner and more crowded just beyond membrane, and then shorter, to terminate some distance behind tip.

Comments

In adult specimens the tuberculation of the chelae is the most obvious feature. In the 1st pleopods of small males (Fig. 3*H*), the tip is relatively short, with fewer bristles on inner and outer sides, but the characteristic row of upper bristles is still present.

Distribution

Known from south-east Africa to Japan, with previous Australian records from Queensland (Rathbun 1923; Ward 1941) and New South Wales (Ward 1941); now from Western Australia.

Charybdis (Charybdis) orientalis Dana, 1852

Figs. 2*B*, 3*B*; Plate 3, Fig. 1; Plate 4*G*

Charybdis (*Charybdis*) *orientalis* Leene, 1938, pp. 68–72, figs. 32–34 (excluding some synonymy); also p. 17.

Charybdis orientalis Sakai, 1939, pp. 407–8, pl. LXXXIII, fig. 2. Barnard, 1950, pp. 170–1, fig. 32*d–g*.

non *Charybdis orientalis* Rathbun, 1906, p. 872 (part) (= *C. hawaiensis* Edmondson, 1954, pp. 249–51, figs. 24*a–c*, 25*a–d*).

non *Charybdis orientalis* Edmondson, 1946, p. 281, fig. 173*e* (= *C. hawaiensis*).

Material Examined

QUEENSLAND: At Zool. Dept., Univ. Qld.: ♀ 46 mm, recently moulted, Mooloolabah, recd. 2.xii.52, coll. during spear-fishing, F. Maiden; ♀ 27 mm, Burleigh, south Qld., 27.v.53, coll. Misses M. Martin and B. Winks, L.W.S., in sand near rocks; ♀ 39 mm,* under stones, M.L.W., Shoal Pt., Mackay, 24.viii.53, coll. Zool. Dept. party. At Qld. Mus.: 2 ♂♂ (36, 41* mm), Barron Beach, Cairns, 19.xi.40, coll. A. A. Read (regd. No. W1168). At Aust. Mus.: ♀ 26 mm, 10 fm, Great Sandy Str. off Pt. Inskip (regd. No. E3151—Rathbun's holotype of *C. incisa*).

Material illustrated.—Photograph: starred female. Male pleopod: starred male.

Male Pleopod

Inner spines, viewed from above several are visible below membrane; in the region of the membrane inner and upper bristles can scarcely be resolved into their series. Here 5 or 6 normal bristles and a roughly equal number of small bristles or spinules are present. Outer bristles fairly long, somewhat irregularly spaced, becoming regularly spaced and progressively shorter beyond membrane.

Comments

Edmondson (1954) has followed up and confirmed a suggestion by Chace (in Leene 1938) that the Hawaiian form might be a separate species. Rathbun's *C. incisa* differs from typical *C. orientalis*, as figured by Leene, only by possessing rounder frontal lobes, with the submedians slightly broader in proportion. The fact that no similar specimen has appeared in Australian collections (or elsewhere) since Rathbun's time also tends to confirm Leene's suggestion that *C. incisa* should disappear into the synonymy.

Distribution

From east Africa to Japan. Previously recorded from Queensland (Stephenson and Stephenson 1931; Ward 1941) and New South Wales (Haswell 1882; Ward 1941), but probably some of these records are of misidentified *C. helleri*, to which the present species has a superficial resemblance.

CHARYBDIS (CHARYBDIS) VARIEGATA (Fabricius, 1798)

Fig. 3*C* (from Leene 1938); Plate 3, Fig. 2

Charybdis (*Goniosoma*) *variegata* Chopra, 1935, pp. 488–9, fig. 10 (male pleopod).
Charybdis (*Charybdis*) *variegata* Leene, 1938, pp. 84–8, figs. 44, 45.
Charybdis variegata Sakai, 1939, pp. 406–7, pl. XLVII, fig. 4. Barnard, 1950, p. 170, fig. 32*c*.

Not seen in present collections, but recorded from Northern Territory (Henderson 1893, fide Leene 1938).

Male Pleopod (after Chopra and Leene)

Membrane near tip. Inner spines, a sparse row beginning as spinules and ending as short spines just beyond membrane. Upper spines, up to 2 large and a row of 5 small spines. Outer spines, best visible from under surface; spinules increasing in size to form moderately long spines opposite membrane, then decreasing in size to give a clump of small spines just behind tip.

Comments

See *C. callianassa*.

Distribution

Persian Gulf to northern Australia.

CHARYBDIS (GONIOHELLENUS) TRUNCATA (Fabricius, 1798)

Figs. 2*D*, 3*E*; Plate 3, Fig. 3; Plate 4*I*

Charybdis (*Goniohellenus*) *truncata* Leene, 1938, pp. 118–21, figs. 66, 67.
Charybdis truncata Sakai, 1939, pp. 412–13, pl. XLV, fig. 4.

Material Examined

4 ♂♂ (23–59 mm); 7 ♀♀ (19–48 mm). Smallest ovigerous ♀ 38 mm, from month of April. *Sacculina* infection, 20 per cent.

QUEENSLAND: Mappoon, Magnetic I., Platypus Bay, Bowen. WESTERN AUSTRALIA: Exmouth Gulf.

Recorded habitats.—Trawled 5–10 fm.

Material illustrated.—All at Zool. Dept., Univ. Qld. Photograph: ♂ 49 mm, south Qld., collector unknown. Male pleopod: whole mount, ♂ 44 mm, Magnetic I., near Townsville, Feb.–Mar. 1953, coll. R. K. Bryson; tip, ♂ 23 mm, other data as last specimen.

Male Pleopod

Inner spines, best visible from the under surface as a series of spinules becoming longer and closer to the upper surface eventually to give 4 or 5 normal bristles

opposite and partly hidden by membrane. Upper spines, a regular row of 9–12 spinules mostly covered by the membrane and invisible in a whole mount, with an occasional small isolated bristle. Outer spines, beginning well back as long, stout, feathered (pinnate) bristles and becoming plain bristles progressively shorter, opposite membrane.

Comments

Leene's (1938, Fig. 66) figure shows the penultimate segment of the male abdomen too short and its sides too rounded. The sharp posterolateral borders and the granulated chelipeds of the species are easily recognizable.

Distribution

From India and the Maldives to Japan, with previous records from Queensland (Rathbun 1923) and Northern Territory (Miers 1884), but not from Western Australia.

Charybdis (Gonioneptunus) bimaculata (Miers, 1886)

Figs. 2*J*, 3*K*; Plate 3, Fig. 4; Plates 4*H*, 5*A*

Charybdis (*Gonioneptunus*) *bimaculata* Leene, 1938, pp. 126–9, figs. 70, 71.
Charybdis bimaculata Sakai, 1939, pp. 410–12, figs. 10, 11 (synonymy).
Charybdis (*Gonioneptunus*) *subornata* Leene, 1938, pp. 122–5, figs. 68, 69.
Charybdis (*Gonioneptunus*) *whiteleggei* Ward, 1933, p. 380, pl. 23, figs. 1, 2. Leene, 1938, pp. 125–6.

Material Examined

8 ♂♂ (5–41 mm).

QUEENSLAND: Warrior Reef. NEW SOUTH WALES: Botany Bay, Watamooli, Newcastle, Pt. Perpendicular, Wreck Bay.

Recorded habitats.—Trawled, 30–72 fm.

Material illustrated.—Photograph and male pleopod: ♂ 35 mm, 40–50 fm, off Newcastle, pres. Aug. 1935, coll. M. Ward (Aust. Mus. regd. No. P10627).

Male Pleopod

Inner spines, a sparse irregular band best seen on the under surface, visible as 4–8 bristles in membrane region; upper spines, 2 rows, extending down behind and hidden by the membrane; outer spines, beginning well down the appendage, somewhat sparsely arranged, from long to moderate-sized, and extending to just behind tip.

Comments

After examining Japanese specimens of *C. bimaculata* in the Australian Museum, and also the above collection, which includes Ward's type of *C. whiteleggei*, there seems little doubt that *C. bimaculata*, *C. subornata*, and *C. whiteleggei* are synonyms.

This is further supported by the absence of significant differences between Leene's descriptions and figures of the male pleopods of *C. bimaculata* and *C. subornata*. In both, the pleopods are figured as being stouter than those of the present specimens, and in both fewer bristles are shown on the outer sides of the appendage. Sakai (1939, Fig. 11) has shown the variations in the pleopod with increasing size of specimens.

Distribution

From India and the Maldives to Japan, with previous records from New South Wales (Ward 1933) but not Queensland.

IV. Discussion

The first male pleopods in this genus have a fairly uniform structure, especially within the subgenus *Charybdis*, but the differences still serve to separate the species. As in *Thalamita*, species which resemble each other in general features also show resemblances in pleopod structure (Stephenson and Hudson 1957). There are insufficient data to warrant the erection of species groups, but pleopod structure does show relationships between three different groups of species, as follows:

(*a*) *C. jaubertensis* and *C. orientalis*, possessing protruding lips;

(*b*) *C. variegata* and *C. callianassa*, with the membrane near the lips;

(*c*) The remainder, comprising *C. cruciata*, *C. lucifera*, *C. natator*, *C. miles*, *C. helleri*, and *C. orientalis*.

The distribution of the genus is probably less completely known than that of *Thalamita* because, with the exception of the intertidal *C. helleri*, the genus characteristically inhabits sublittoral environments. Sublittoral collections in Australian waters have not been extensive, and many of the new State records which are here given result from the recent extensions in prawning grounds.

In the case of five species (*C. anisodon*, *C. lucifera*, *C. miles*, *C. variegata*, *C. truncata*) there are too few records for biogeographical discussion, and in a sixth (*C. orientalis*) some of the published records are suspect. The remaining six species are recorded from both the east and west coasts of Australia, and extend further south on the east than on the west. This suggests that the southerly extension of these Indo–West Pacific species is limited by water temperatures, and if so they can be arranged as follows in order of increasing tolerance to lower temperatures: *C. helleri*, *C. callianassa*, *C. jaubertensis*, *C. natator*, *C. cruciata*. On the east coast at Moreton Bay, and on the west coast at Exmouth Gulf, there is a sufficient concentration of southerly limits for these almost to be considered as biogeographical boundaries.

V. Acknowledgments

We are deeply grateful to the numerous collectors of specimens whose names we have been obliged to exclude for reasons of brevity, and without whose endeavours this paper could scarcely have been written. We are also deeply grateful to the following Museums and their Directors for allowing us to examine their collections, and to borrow specimens and literature: Australian Museum, Sydney (Dr. A. B. Walkom and later Dr. J. W. Evans); Queensland Museum (Mr. G. Mack); Western Australian Museum (Mr. L. Glauert); National Museum, Melbourne (Mr. R. T. M. Pescott); Macleay Museum, University of Sydney (Mr. J. R. Henry); Museum of the Zoology Department, University of Melbourne (the late Professor O. W. Tiegs); and South Australian Museum (Mr. H. M. Hale).

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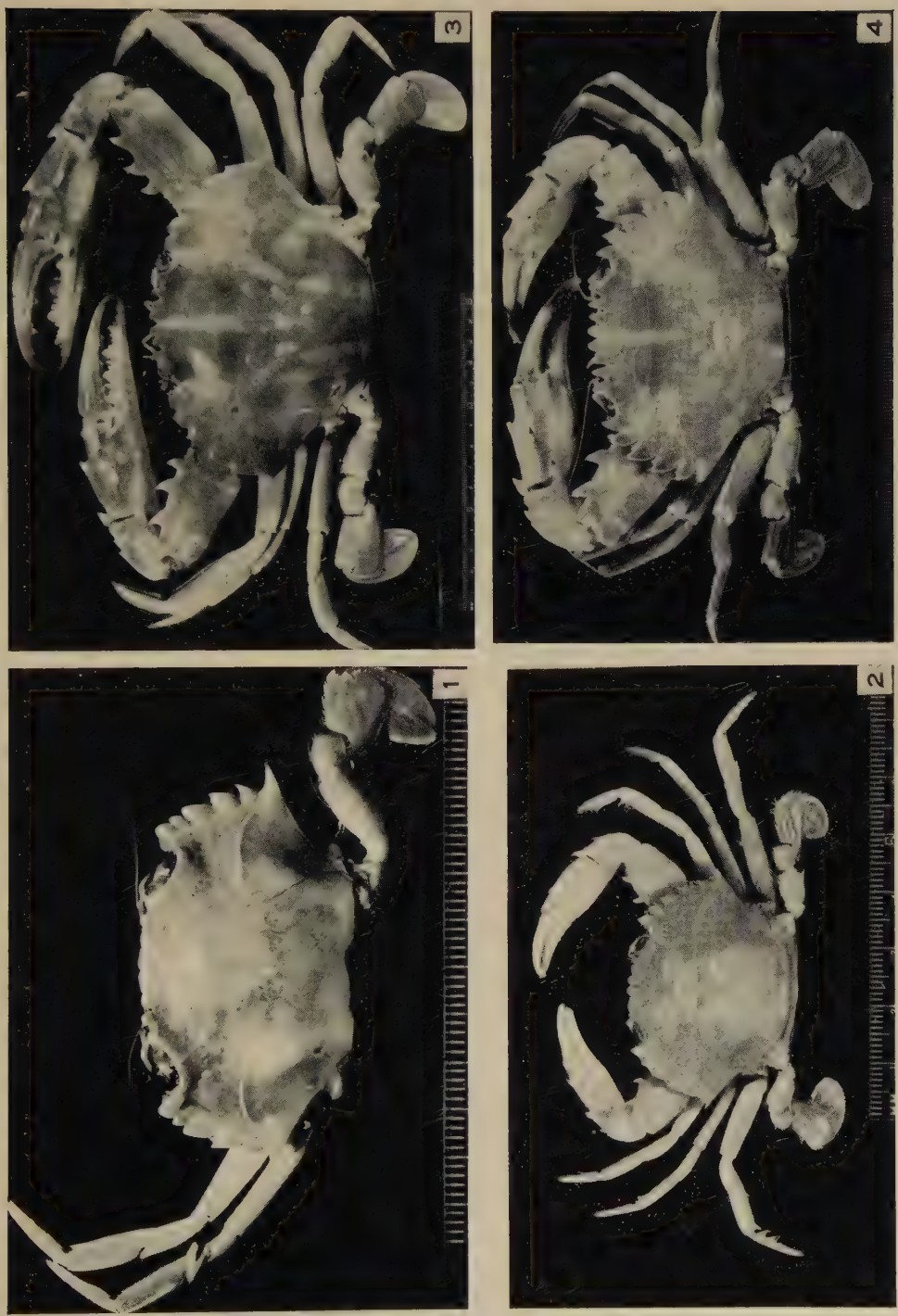
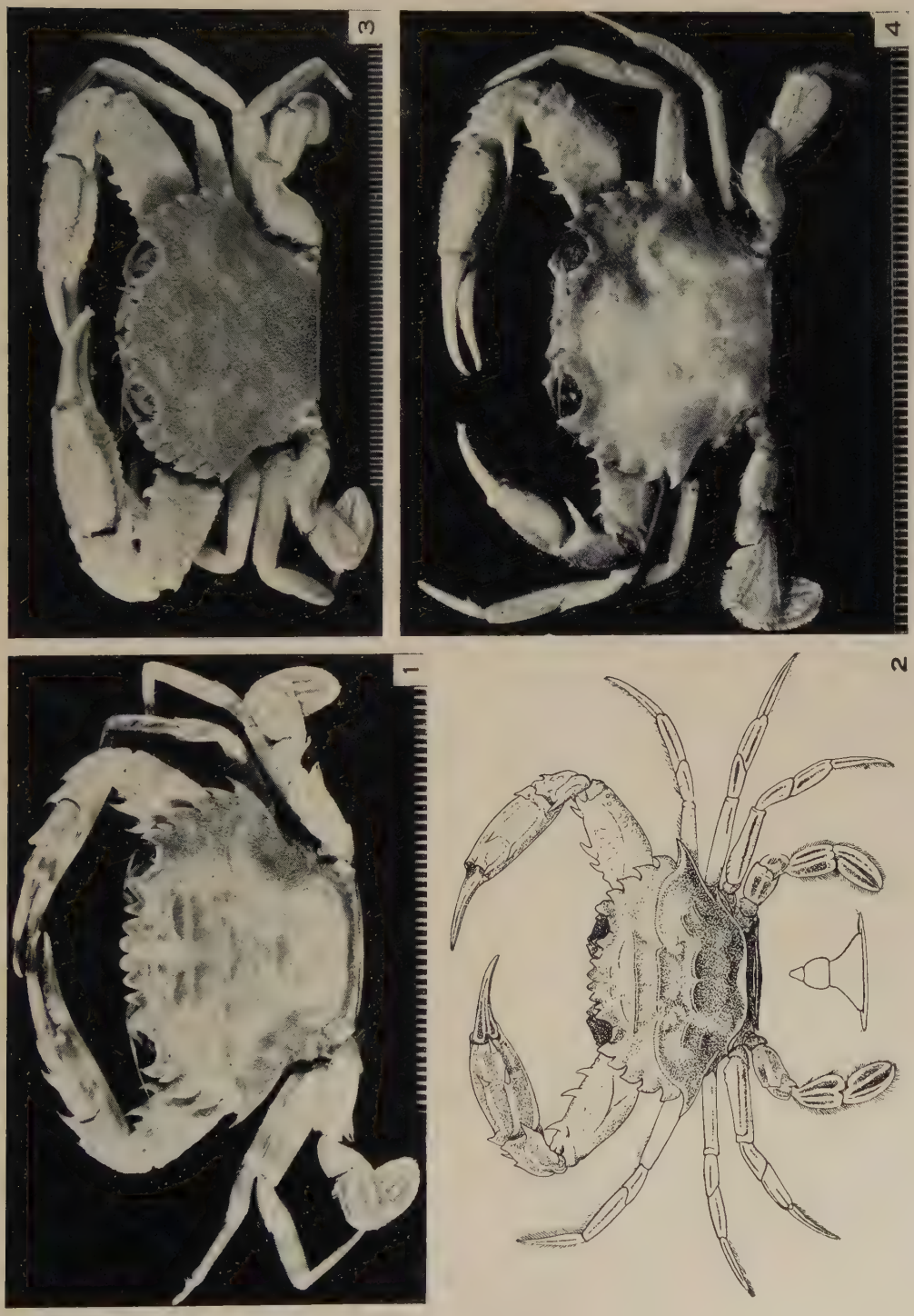


Dorsal views of *Charybdis* spp. Scale divisions, 1 mm. Fig. 1.—*C. anisodon*. Fig. 2.—*C. cadlianassa*. Fig. 3.—*C. cruciata*. Fig. 4.—*C. helleri* (reproduced from Leene (1938)).

AUSTRALIAN PORTUNIDS. II

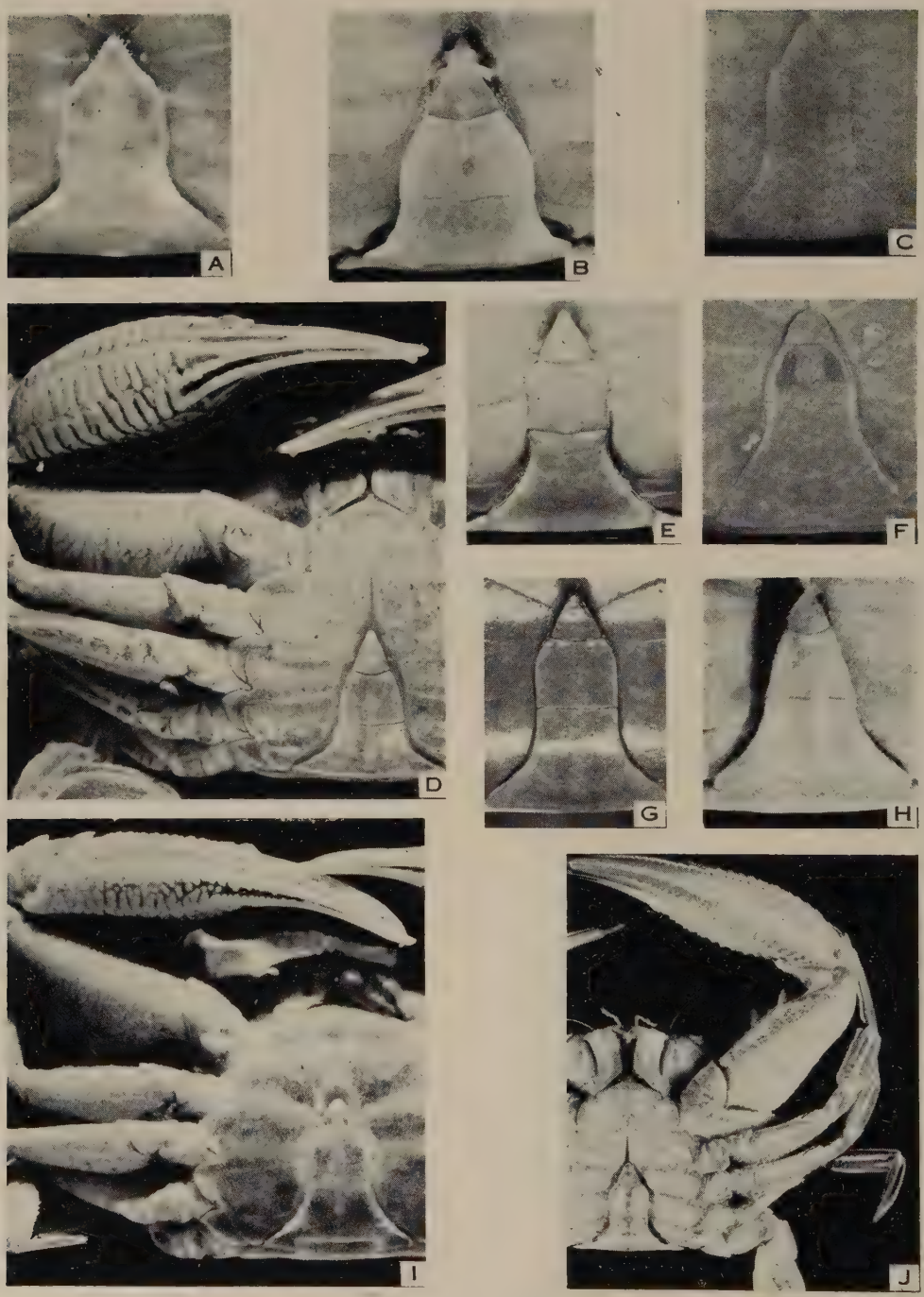
Dorsal views of *Charybdis* spp. Scale divisions, 1 mm. Fig. 1.—*C. jaubertensis*. Fig. 2.—*C. lucifera*. Fig. 3.—*C. miles*. Fig. 4.—*C. natator*.

AUSTRALIAN PORTUNIDS. II



Dorsal views of *Charybdis* spp. Scale divisions, 1 mm. Fig. 1.—*C. orientalis*. Fig. 2.—*C. variegata*. Fig. 3.—*C. truncata*. Fig. 4.—*C. bimaculata*.

AUSTRALIAN PORTUNIDS. II



Male abdomens and, in *D*, *I*, *J*, under surface of chelae. *A*, *C. callianassa* ; *B*, *C. cruciata*; *C*, *C. helleri*; *D*, *C. jaubertensis*; *E*, *C. lucifera*; *F*, *C. miles*; *G*, *C. orientalis*; *H*, *C. bimaculata*; *I*, *C. truncata*; *J*, *C. natator*.

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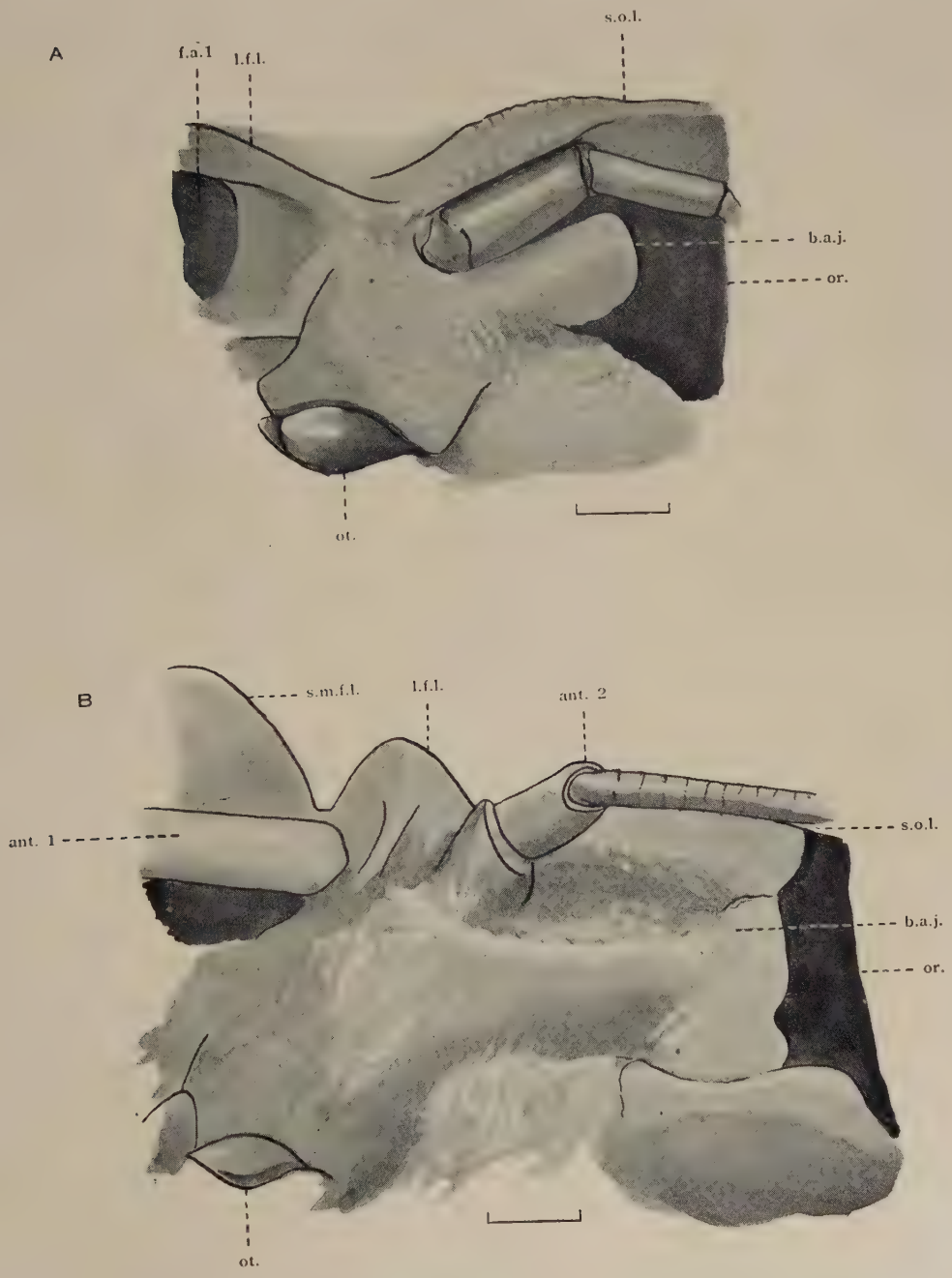

Basal antennal joints. *A*, *C. bimaculata*, showing second antenna within the orbit. *B*, *C. helleri*, with second antenna excluded from the orbit. Scale divisions, 0·5 mm. *ant.* 1, First antenna; *ant.* 2, second antenna; *b.a.j.*, basal antennal joint; *f.a.*1, fossa of first antenna; *l.f.l.*, lateral frontal lobe; *or.*, orbit; *ot.*, otolith; *s.m.f.l.*, submedian frontal lobe; *s.o.l.*, supra-orbital lobe.

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THE BREEDING CYCLE OF THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By R. G. Chittleborough*

[*Manuscript received August* 12, 1957]

Summary

The gestation period in the humpback whale is of almost 12 months' duration, most conceptions occurring early in August with parturition at the beginning of the following August. The modal length of calves at birth is 14 ft. The sex ratio at birth is 51·4 per cent. males to 48·6 per cent. females. Twin foetuses are occasionally recorded. There is no preference towards either right or left ovary or uterine cornu with regard to ovulation or pregnancy. The breaking of the umbilical cord at birth is described.

The histological appearances of the mammary gland during advanced pregnancy and during lactation are described and illustrated. Upon the evidence presented it is concluded that lactation in this species extends over 10½ months, suckling generally commencing in mid August and terminating at the end of the following June. The composition of the milk has been determined during various stages of lactation.

Oestrous cycles rarely occur during pregnancy, but examples of ovulation following shortly after parturition, while the females are suckling their calves, are cited. It is shown that when the calf is lost at or soon after birth, oestrous cycles usually recommence at once. Where the calf is suckled for the normal period (10½ months) there is no anoestrous period following the end of lactation as oestrous cycles recommence in July, immediately after (occasionally just before) weaning at the end of June.

Three types of breeding cycle are shown for the humpback whale. In the most common cycle, absence of the post-partum ovulation, or its occurrence without conception, results in one calf in 2 years. On the other hand, a successful post-partum ovulation results in two calves in 2 years. In the third type of cycle, loss of the first calf at or just after parturition is balanced by a second pregnancy succeeding immediately afterwards. This results in two pregnancies in 2 years with only one calf reared.

I. Introduction

Southern humpback whales feed during the summer in Antarctic waters and migrate northwards each autumn to spend the winter months in tropical and sub-tropical regions (Matthews 1937; Mackintosh 1942). It is probable that most, if not all, individuals take part in this seasonal migration. Australian coastal whaling stations take fixed quotas of these whales between June and October, while in the Antarctic the catching of humpback whales is at present permitted during the first 4 days of February.

Owing to their size and habits it is not possible to make repeated observations upon individual humpback whales in order to determine the length of the gestation period and the duration of lactation. To establish the times of occurrence and duration of these phases one must obtain evidence from a large number of individuals killed at varying stages and then decide the most probable normal sequence of events in the species.

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The only real attempt to do this for humpback whales was that of Matthews (1937), who suggested that gestation occupied about 11 months, most conceptions occurring in September with parturition the following August. The body length at birth was considered to lie between 4·5 and 5·0 metres (14 ft 9 in. to 16 ft 5 in.). On the very limited evidence available, Matthews proposed that the calf was suckled for approximately 5 months. A breeding cycle of one calf in 2 years was given for this species, the majority of the first year being occupied by pregnancy, the first 5 months of the second year in lactation, and the remaining 7 months in non-lactating anoestrus. It was suggested that in a few females ovulation might occur at the end of the 5 months' lactation, so that in some cases two pregnancies would occur in 3 years.

From the material collected in recent years (1949–1955) at shore-based whaling stations on the west coast of Australia, these findings may now be reviewed and extended.

II. Material

The results given in this paper are based primarily upon 390 sexually mature female humpback whales examined in detail by the author. Further valuable information was obtained from the ovaries collected by whaling inspectors from 287 mature females. These females were sampled at random from the normal catches at Western Australian whaling stations. In addition, three females and their calves were killed under special licence for research purposes and fully examined by the author.

Certain aspects of the results obtained from these whales have already been published (Chittleborough 1954, 1955).

In this paper the records kept by whaling inspectors of all foetuses found (at Western Australian whaling stations) between 1949 and 1955, have been examined for certain aspects of pregnancy and parturition. Also with reference to parturition, the results of aerial observations upon 1765 adult humpback whales have been used. An account of some of these aerial observations has already been published (Chittleborough 1953).

Records of foetuses from Antarctic areas IV and V (from 1949 to 1956) (see Mackintosh (1942) for definition of areas) were obtained from catch returns supplied by International Whaling Statistics, Sandefjord, Norway.

Material from mammary glands for histological examination was fixed in Heidenhain's Susa fixative, and paraffin sections were cut at 7 μ and stained with haematoxylin and eosin. As a rule a sample from the centre of the mammary gland was taken to represent the condition of the whole gland, but in several cases anterior, central, and posterior samples were taken and compared.

Samples of milk from 15 females in progressive stages during and at the end of lactation were taken in bottles of 110 ml capacity, after two drops of commercial formalin (40 per cent. formaldehyde) had been placed in each bottle. The samples were stored in a refrigerator (without freezing) until analysed by the Government Chemical Laboratories of Western Australia.

III. Pregnancy

(a) *Gestation Period*

Early embryos are seldom recorded; since 1949 only two have been obtained from females taken on the west coast of Australia. One small specimen (damaged) was found on September 4, and another on September 8 (crown–rump length 11 mm). Because of the paucity of early embryonic stages, the time of ovulation is considered as an index of the time of conception.

Table 1

HUMPBACK FOETUSES FROM ANTARCTIC AREAS IV AND V, 1949–1956: LENGTH FREQUENCY DISTRIBUTION

Foetal Length (ft)	Year:	1949–50	1951	1952	1953	1954	1955	1956
		Number of Foetuses Recorded						
	Catching Period:	Dec. 16 to Jan. 5	Feb. 2–8	Feb. 1–5	Feb. 1–4, 16–18	Feb. 1–4	Feb. 1–4	Feb. 1–4
0·5		2	1			1		
1		80	19	18		6	5	26
1·5		44	2	4	2	5		6
2		127	71	46	13	12	11	59
2·5		24		4		8	18	8
3		29	115	65	37	18	27	62
3·5		2	3	2	7	11	19	17
4		1	103	55	42	14	21	52
4·5					4	2	4	5
5			35	7	25	1	9	6
5·5						1		1
6		2	2	4	4		9	1
7		1					1	
8		1					2	
11			1					
Mean length (ft):		1·9	3·2	3·0	3·7	2·9	3·5	2·8

In a previous paper (Chittleborough 1954) it was shown that: (1) ovulation in the female humpback whale may occur from the beginning of June until early October; (2) most females (approximately 70 per cent.) ovulate only once during this period; (3) most ovulations occur in the latter part of July and early in August (Fig. 8 of the above paper). From these facts it may be deduced that on the west coast of Australia most pregnancies commence early in August. A number of females may become pregnant later in August or in September, either from a second ovulation or in some cases as a result of a first ovulation which was slightly later than usual.

In catches from Antarctic waters during the southern summer, high proportions of pregnant females are taken. Table 1 shows the length frequency distribution of 1452 foetuses recorded from Antarctic areas IV and V from 1949 to 1956.

When pregnant females return to the Australian coast in the following winter, they are generally in more advanced stages of pregnancy. From 1949 to 1955, 250 foetuses have been recorded from catches on the west coast of Australia. Figure 1 shows the length and date of killing of each foetus, and the length frequency distribution. With one exception (discussed later) these foetuses were close to term.

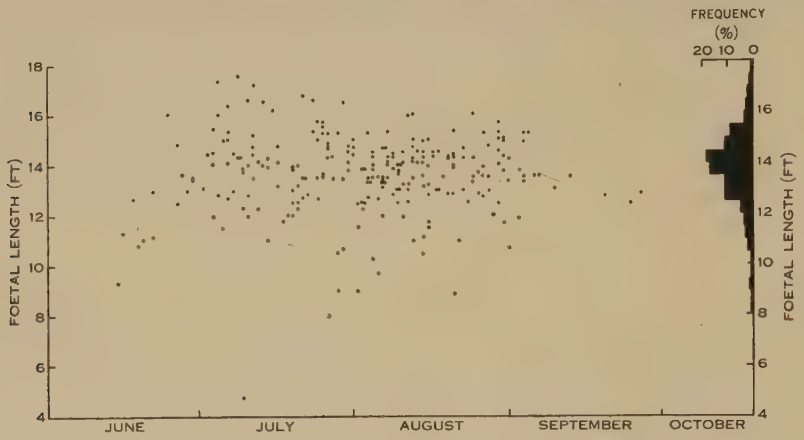

Fig. 1.—Foetal lengths and length frequency distribution of foetuses from the Western Australian coast, 1949–1955.

Figure 2(*a*) shows the distribution of these near-term foetuses as recorded throughout the catching period (June–October). Very few are recorded during June, in spite of high proportions of sexually mature females in the catches for that month.

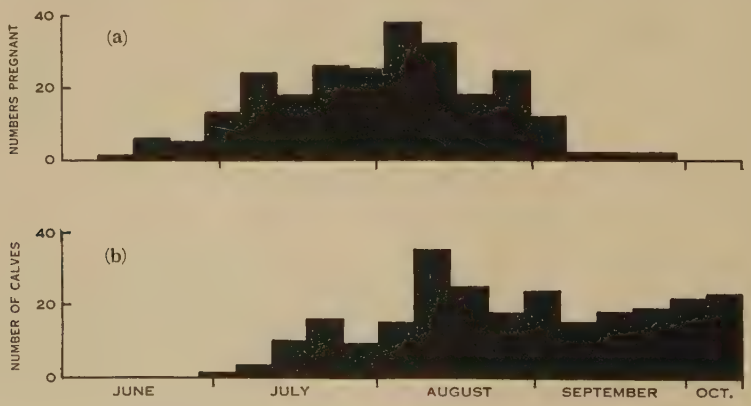

Fig. 2.—(*a*) Distribution of 249 females in advanced pregnancy taken on the Western Australian coast between June and October from 1949 to 1955. (*b*) Distribution of 253 new-born calves sighted amongst 1765 adult humpback whales observed from the air off Point Cloates during 1952 and 1953.

This indicates that females in advanced pregnancy are relatively late in reaching this coast during the northward migration. Figure 2(*a*) shows that females in advanced pregnancy are of most frequent occurrence (off this coast) during July and early

August, but that numbers fall from mid August, apparently as increasing numbers of births occur.

Another approach to the time of parturition is by recording the presence of new-born calves observed amongst the adults moving along the coast. Aerial observations of this kind were made in the region of Point Cloates in 1952 and 1953. A total of 1765 adult humpback whales were checked (from the air), and 253 new-born calves were recorded. The weekly occurrence of the calves throughout the catching period is shown in Figure 2(*b*). This indicates that the first calves are born towards the end of June, slightly more in July, and maximum numbers in August.

By comparing the distribution of near-term foetuses (Fig. 2(*a*)) with that of new-born calves (Fig. 2(*b*)), it can be said that in the humpback whale parturition occurs on the west coast of Australia between June and October, but with a maximum frequency early in August.

From the available data upon ovulation and parturition, as discussed above, the average length of the gestation period in this species is close to 12 months, both conception and parturition occurring with maximum frequency early in August.

(*b*) *Length of Calf at Birth*

Since calves are protected by law it is seldom possible to obtain the length at birth from direct observations. One new-born calf, taken on August 3, 1955, was 15 ft 3 in. in length. From the condition of the uterus of the cow and the unhealed umbilicus of the calf, parturition had taken place approximately 1 week earlier.

The mean length of 249 near-term foetuses taken on the west coast of Australia was 13 ft 8 in. However, this must be slightly below the mean length at birth since at least some of these foetuses would have increased in length in the short time remaining before parturition. The lengths of near-term foetuses shown in Figure 1 are of almost normal distribution round a modal length of 14 ft. This indicates that the size at parturition is normally distributed round that length. From the material examined there does not appear to be any difference between the lengths of males and females at birth.

(*c*) *Foetal Sex Ratio*

Of 249 near-term foetuses taken on the west coast of Australia from 1949 to 1955, 51·4 per cent. were males. From the Antarctic (roughly at mid pregnancy) 1448 humpback foetuses were sexed in catches from areas IV and V between 1949 and 1956; 51·9 per cent. of these foetuses were males.

(*d*) *Multiple Pregnancies*

Multiple pregnancies have occasionally been recorded in the humpback whale (Matthews 1937). Of 1449 pregnant humpback whales listed in the International Whaling Statistics from Antarctic areas IV and V in seasons 1949–50 to 1955–56, only four cases (0·28 per cent.) of twinning were recorded. Since 1949 only one multiple pregnancy (twin female foetuses) has been recorded from humpback whales taken on the Australian coast. Two examples of multiple ovulations have been described (Chittleborough 1954).

(e) *Prevalence of Ovulation and Pregnancy on a Particular Side of the Body*

In some whales taken off the west coast of Australia, ovulations had been predominantly from one ovary, the right in some individuals and the left in others. However, in 148 sexually mature females, a total of 613 ovulations had occurred from the left ovary and 655 from the right. This distribution does not differ significantly from a random one. In 22 pregnant females the 22 corpora graviditata were equally distributed between right and left ovaries, and implantation had always occurred on the same side as the ovulation.

(f) *Breaking of the Umbilical Cord*

In the near-term foetus the normal skin on the ventral surface of the body extends up to 7 in. along the umbilical cord, covering the cord in this region. On several occasions when a near-term foetus slid from the uterus during cutting operations, the pulling of the foetus against the placenta caused the umbilical cord to break. In each case the break occurred cleanly against the body wall, so that all that remained attached to the foetus was an empty tube of the skin which had previously enveloped the base of the cord. The same condition was found in a new-born calf. It is probable that the cord normally breaks here during parturition. Van Utrecht (personal communication) has made similar observations upon new-born young of the white-sided dolphin (*Lagenorhynchus acutus* (Gray)).

(g) *Mammary Glands During Advanced Pregnancy*

In pregnant females close to parturition the lobules and alveoli of the mammary glands are well developed and in most cases fluid is present in the ducts. This is often a clear liquid, slightly yellow or pale brown in colour, or sometimes turbid and white, looking like much diluted milk. Large quantities may be present at this stage, the fluid often spurting from the nipples as the pregnant female is hauled from the water.

Histologically two phases could be distinguished in the mammary glands of pregnant females close to parturition. One phase (see Plate 1, Fig. 1) was characterized by the large vesicular nuclei of the alveolar cells, the cytoplasm of which stained very little (with haematoxylin or eosin). These cells showed little sign of secretory activity. The lumina of the alveoli were generally empty, except that scattered alveoli contained a non-granular acidophilic secretion, which was also present in some ducts. This fluid may be similar to the globulin secretion produced in the mammary glands from mid pregnancy in goats (Drummond-Robinson and Asdell 1926).

In the second phase (see Plate 1, Fig. 2) the nuclei of the alveolar cells were generally slightly smaller, non-spherical, and darker-staining with more concentrated chromatin. The cytoplasm was more granular and basophilic, while occasional clear droplets in the cytoplasm suggested that globules of fat (removed during the preparation of sections) were being secreted. Within the alveoli there was abundant granular basophilic material with a few fat globules. Secretory activity was greater in peripheral alveoli within each lobule.

It would appear that these two phases follow each other in the order given above, the second phase approaching the histological appearance of the mammary glands of actively lactating females. The second phase is probably reached very shortly before parturition. If this is so, one foetus 12 ft 7 in. long was very close to term.

IV. Lactation

(*a*) *Characteristics*

As pointed out by van Lennep and van Utrecht (1953) there is considerable confusion regarding the characteristics and definition of lactation in whales. In its true sense a lactating female is suckling a calf, but once the whale is on the flensing deck it is difficult to establish positively that a female whose mammary glands are milk-filled had in fact been accompanied by a suckling calf up to the time of killing.

In the present work the first criterion of lactation was the presence of apparently normal milk. Other fluids—for example, the less dense and often discoloured liquid as often found in the mammary ducts during advanced pregnancy, or the rather white watery fluid found in some glands involuting after lactation—were not classed as milk. The quantity of normal milk is of little diagnostic value. Soon after parturition the calf may be feeding frequently, so that a female killed early in lactation might not be carrying much milk in the ducts although lactating heavily. This was found in one case (discussed later) where a female and its young calf were taken. On the other hand during the weaning period the calf may suckle less regularly, so that milk may accumulate in the mammary glands, even to the extent that it is forced from the nipples as a female in late lactation is hauled from the water. Also if the calf is lost the milk would temporarily accumulate in the female's mammary glands. Accordingly the presence of large quantities of milk is not necessarily proof that a suckling calf was present when the female was killed.

As a second criterion of lactation the histological appearance of the mammary glands was considered. It has been shown in the guinea-pig (Hesselberg and Loeb 1937) and the mouse (Williams 1942) that some involutional changes begin in the mammary glands shortly before weaning, apparently as a result of lessened suckling. Thus if the mammary glands are actively secreting and show no signs of involution, the young are still suckling. This interpretation was followed with those humpback whales whose mammary glands contained apparently normal milk. If the alveoli of the glands showed no sign of involution and the cells lining the alveoli were actually secreting, the female was classified as still suckling the calf. If the ducts contained milk and the alveolar cells were no longer secreting (generally with signs of resorption of the alveolar cells) it was considered that the female had either recently lost, was weaning, or had just finished weaning the calf, and that the apparently normal milk present in the ducts was a residuum which would have shortly disappeared.

In several cases where milk was present, samples of mammary gland tissue from anterior, central, and posterior regions of the glands were preserved in order to compare the activity of the various regions. The condition of the lobules was generally found to be uniform throughout the gland, although in one female killed at the end of lactation, involution of the lobules in the posterior region of the mammary gland appeared to be slightly in advance of that of lobules in the anterior part of the gland.

The condition of the ovaries gives some indication of how recently parturition has occurred. Soon after parturition the corpus luteum of pregnancy is still large and, though involuting, shows evidence of its recent activity (see Plate 2). Towards the end of the suckling period the resorption of the recently functional corpus luteum

is so far advanced that it must be classed as a corpus albicans, and is often reduced to such an extent that it is difficult to decide which corpus albicans had been functional most recently (Chittleborough 1954).

If parturition has only recently occurred the uterus may still be somewhat enlarged, with a thickened fibrous wall and low pointed glandular folds in the endometrium. However, after parturition the uterus usually returns rapidly to a similar size and structure as before the pregnancy, so that the condition of the uterus is a useful diagnostic feature for only a brief period after parturition.

(*b*) *Duration of Lactation*

Since in most cases parturition takes place early in August (Section III(*a*)), it is suggested that most females have begun lactating by mid August.

TABLE 2

FEMALES WITH MILK BUT SHOWING NO EVIDENCE OF RECENT PARTURITION: INCIDENCE AMONGST 348 SEXUALLY MATURE FEMALES TAKEN ON THE WESTERN AUSTRALIAN COAST (1949–1955)

Ten-day Period	Total Mature Females Examined	Females with Milk but No Evidence of Recent Parturition	
	No.	No.	Percentage
June 1–10	26	19	73·1
June 11–20	64	48	75·0
June 21–30	31	24	77·4
July 1–10	20	6	30·0
July 11–20	35	8	22·9
July 21–30	16	1	6·3
July 31–Aug. 9	41	3	7·3
Aug. 10–19	18	1	5·6
Aug. 20–29	23	0	0·0
Aug. 30–Sept. 8	35	2	5·7
Sept. 9–18	21	2	9·5
Sept. 19–28	10	1	10·0
Sept. 29–Oct. 8	8	1	12·5

Regarding the termination of lactation, it has been found that many sexually mature, non-pregnant females taken on the west coast of Australia in June and early July of each year carry milk in the mammary glands (Chittleborough 1954). The ovaries and uteri of these females were generally in a resting (anoestrous) condition, indicating that the previous birth had occurred some months before. In a few cases a Graafian follicle was maturing, or ovulation had recently occurred.

Table 2 and Figure 3 show the percentages of females whose mammary glands contained normal milk and which showed no sign of a recent birth, amongst sexually

mature, non-pregnant females taken in each 10-day period from June to October. Figure 3 indicates that most mature, non-pregnant females are lactating in June, but that lactation usually ceases by the beginning of July.

However, as stressed in the previous section, the presence of milk is not proof in itself that a calf is being suckled, but the cytological condition of the mammary glands affords some confirmatory evidence that suckling is proceeding. Many of these females in milk had been dead too long to allow a satisfactory histological examination. The mammary glands were sectioned in 22 specimens of freshly killed females whose glands contained milk but which showed no evidence of a recent birth. The glands of 17 of these, all killed during June and the first week of July, were fully developed and secreting, having the same microscopic appearance as the glands during early lactation (compare Figs. 1 and 2 of Plate 3). The mammary glands of the remaining five, all killed after the first week of July, were regressing and cells lining the alveoli were no longer secretory (see Plate 4, Fig. 1). This suggests that these females had recently weaned their calves.

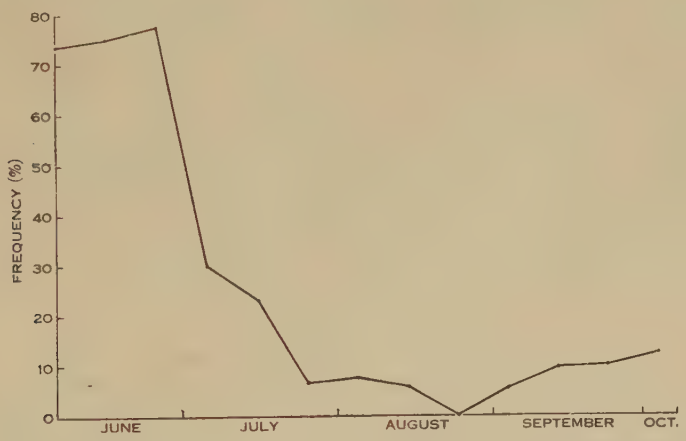

Fig. 3.—Females with milk but no evidence of recent parturition: percentage frequency amongst sexually mature females examined on the Western Australian coast from 1951 to 1955.

To sum up, most of the mature non-pregnant females killed on the west coast of Australia during June have enlarged mammary glands containing milk. The alveoli of these glands are lined with actively secreting cells, indicating that these females are suckling calves. The ovaries and uteri indicate that the previous birth had occurred some months ago. The gunners of the whaling vessels on this coast report that during June many females are accompanied by "yearling" calves. The stomachs of two such "yearlings" (one female 29 ft 3 in. in length shot on June 12, the other, also female, 28 ft 9 in. in length, shot on June 14) were found to contain partly digested milk, proving that these were still suckling.

The above evidence indicates that most young are suckled until the end of June. From Table 2 and Figure 3 it is inferred that most young are weaned towards the end of June or the beginning of July.

TABLE 3

COMPOSITION OF MILK AND MILK RESIDUES FROM 15 FEMALE HUMPBACK WHALES FROM THE WEST COAST OF AUSTRALIA

Stage of Lactation		Date Whale Killed	Composition of Milk					
			Specific Gravity	Total Solids (%)	Fat (%)	Protein (N × 6·38)	Ash (%)	Carbohydrate* (%)
Suckling new-born calf (approx. 1 week after parturition)		3.viii	1·042	35·6	20·4	12·4	1·6	1·2
Just prior to weaning: mammary glands actively secreting		13.vi	1·030	47·1	29·1	—	1·94	—
		14.vi	1·004	54·7	39·2	13·1	1·56	0·8
		15.vi	1·016	46·8	32·6	12·5	1·53	0·2
		15.vi	1·030	41·8	32·4	—	1·80	—
		16.vi	1·015	54·0	37·0	13·6	1·66	1·7
		17.vi	0·992	54·8	41·3	10·7	1·41	1·4
		18.vi	1·008	47·5	26·6	—	1·39	—
		19.vi	0·958	40·5	25·5	11·8	1·55	1·6
	Mean:		1·007	48·4	33·0	12·5	1·61	1·1
Calves just weaned: alveoli involuting and no longer secretory	Left†	15.vii	0·989	63·6	32·0	—	1·01	—
	Right†	15.vii	0·989	63·8	33·6	—	1·01	—
	Left†	18.vii	1·017	42·9	28·5	—	2·04	—
	Right†	18.vii	1·017	42·1	26·8	—	2·09	—
		18.vii	1·018	47·8	31·8	—	1·49	—
	‡	10.viii	—	58·5	54·3	3·0	0·5	0·7
Recently lactating: mammary glands involuting. Residual fluid in mammary ducts after weaning—oestrus cycles recommenced		2.viii	—	6·1	0·4	4·6	1·0	0·1
	Left	9.viii	—	7·6	0·7	4·7	0·9	1·3
	Right	9.viii	—	18·8	12·9	4·3	0·9	0·7

*By difference.
†Milk thicker than usual.
‡Milk extremely thick.

With lactation generally commencing in mid August and weaning taking place at the end of the following June, the average length of the lactation period in the humpback whale is thus 10½ months.

Contrary to the suggestion by Matthews (1937) no evidence has been found of a sudden increase in the length of baleen plates in young whales at the time of weaning.

(c) *Composition of Milk*

Table 3 shows the results from the analysis of milk and milk residues from 15 female humpback whales in progressive stages during and after lactation. In most cases the analysis was performed on a pooled sample from both mammary glands, but on three occasions samples from left and right glands were collected and analysed separately.

In comparison with later stages, the milk from the female shot at the commencement of suckling was already high in protein content (12·4 per cent.). The fat content was also relatively high (20·4 per cent.) but not as high as that in the milk of females during more advanced lactation.

For a short time after weaning, when the mammary glands are enlarged but no longer secretory, some milk of almost normal appearance and composition is found in the mammary ducts (Table 3). At a later stage after lactation when the involution of the mammary glands is more marked there may be some liquid in the mammary ducts, but this usually has the appearance of whitish or turbid yellowish water. The composition of such fluid from two females in this phase is shown at the bottom of Table 3.

V. Ovarian Cycles

(a) *Ovarian Activity During Pregnancy*

Unlike the horse (Amoroso, Hancock, and Rowlands 1948) and the African elephant (Perry 1953) where secondary corpora lutea are developed and become functional during pregnancy, the one corpus luteum persists throughout pregnancy in the humpback whale. Proof of this was obtained from several young female humpbacks killed towards the end of the first pregnancy, when the ovaries carried but one corpus graviditatis but no corpora albicantia or luteinized follicles.

The records and ovaries examined by the author at the National Institute of Oceanography in England, and the State Institute for Whaling Research in Norway, showed that the Graafian follicles of pregnant humpback whales taken in Antarctic waters (approximately mid pregnancy) are generally of comparable size (diameters from 10 to 30 mm) to those in non-pregnant anoestrous females.

However, when such females return to temperate waters during advanced pregnancy the majority of the previously well-developed Graafian follicles (those over 10 mm in diameter) have atrophied (Chittleborough 1954). The remaining small follicles (generally up to 6 mm but occasionally reaching 10 mm in diameter) are quite normal, having a large antrum lined by granulosa cells and a cumulus enveloping a normal ovum (Plate 5, Fig. 1). Atretic follicles are very abundant in the ovaries

during advanced pregnancy. The ovum within one such atretic follicle had fragmented (Plate 5, Fig. 2). Similar apparent cleavages of ova in atretic follicles have been recorded in other mammals (Boyd and Hamilton 1952, p. 41; Ishida 1953).

In one pregnant female carrying a foetus 12 ft 9 in. in length, Graafian follicles had developed considerably and one follicle 48 mm in diameter was mature. The corpus luteum of pregnancy was in early stages of resorption, similar in size and structure to the condition normally found during early lactation. This case of the initiation of a further ovarian cycle (with resorption of the corpus graviditatis) shortly before parturition must be considered rare in the humpback whale, since in the ovaries of over 70 other females examined during advanced pregnancy there was no development of follicles and no such marked resorption of the corpus graviditatis.

(*b*) *Ovulation Following Parturition Without Loss of Calf*

A lactating female and its young calf were taken on September 15, 1953. The calf, 20 ft 4 in. in length, was considered to be from 2 to 3 months old. The stomach was filled with curdled milk and the intestines contained much bright yellow liquid, so that this calf had been actively suckling.

The maternal mammary glands were actively secreting (Plate 3, Fig. 1) and normal milk was present in the ducts. The recently functional corpus luteum in this female was in early stages of resorption but was still relatively large (95 by 79 by 77 mm), weighing 308 g, and hanging away from the ovary (Plate 2, Fig. 1). In contrast to the general condition during advanced pregnancy, the Graafian follicles of this female in early lactation were well developed, several reaching 22 mm in diameter while one at 34 mm appeared to be maturing. Ovulation had recently occurred, as shown by a developing corpus luteum (59 by 55 by 55 mm), the blood-stained hole at the point of rupture being almost closed by expanding luteal tissue. Thus this female had ovulated soon after parturition.

Another female, killed on August 10, appeared to have recently given birth, as evidenced by a recently functional corpus luteum (104 by 91 by 86 mm, weight 553 g) hanging from one ovary (Plate 2, Fig. 2). The uterine wall was thickened and fibrous, similar to the uterus of the female described above and known to be in early lactation. The mammary glands contained abundant milk and the alveoli were actively secreting. Although the gunner of the catching vessel did not record that a calf was present, the condition of this female strongly indicates that a very young calf was present and being suckled. This female had not ovulated since parturition, but the Graafian follicles were well developed (up to 21 mm in diameter).

Three females taken on the west coast of Australia provided clear examples of post-partum ovulation resulting in pregnancy. When killed (on June 14, 18, and 21 respectively), these females were in advanced pregnancy (foetal lengths 9 ft 3 in., 10 ft 9 in., and 13 ft 0 in.) and yet were in late stages of lactation. In these cases ovulation soon after parturition had resulted in a further pregnancy, so that when killed approximately 10 months after the previous birth they were in advanced pregnancy and also in the last stages of suckling their previous calves.

Further evidence of post-partum ovulation resulting in pregnancy has been obtained from unpublished Norwegian records which the author was permitted to

study. Norwegian observers have carefully examined 94 sexually mature female humpback whales taken in Antarctic waters between 1949 and 1955. These females are listed in Table 4 according to the stage in the breeding cycle.

It must be stressed that the percentages given in Table 4 do not represent a random sample of the sexually mature females, as there had been selection, not only by the gunners but also to some extent by the observers, who tended to pay more attention to any lactating females which were taken rather infrequently. With the above reservation, Table 4 shows two important aspects concerning the breeding cycle of female humpback whales.

TABLE 4

SEXUALLY MATURE FEMALE HUMPBACK WHALES (TAKEN IN THE ANTARCTIC FROM 1950 TO 1955) CLASSIFIED BY NORWEGIAN OBSERVERS INTO THEIR RESPECTIVE PHASE OF THE BREEDING CYCLE

Condition	Number	Percentage
Neither pregnant nor lactating (resting)	8	8·5
Pregnant but not lactating	67	71·3
Pregnant and lactating	8	8·5
Lactating but not pregnant	11	11·7
Total	94	

Firstly, of those sexually mature females permitted to be taken in the Antarctic (either pregnant or "resting"), relatively few are "resting" (neither pregnant nor lactating). These few represent those females which had failed to conceive during the previous ovulatory season. Secondly, of the carefully examined lactating females a surprisingly high proportion were concurrently pregnant, which suggests that post-partum ovulation with successful conception is not uncommon in the humpback whale.

Although at present the number of observations upon such females is too small to allow a detailed comparison to be made, it appears that the foetuses carried by lactating females tend to be slightly smaller than foetuses from non-lactating females killed at the same time. This suggests that pregnancies resulting from post-partum ovulation began a little later (perhaps by a month) than most of the pregnancies which began after the previous lactation period.

(c) *Ovulation Following Parturition, After Loss of Calf*

Six females, killed during August and September, appeared from the state of the ovaries and uteri to have recently given birth. The mammary glands were

enlarged and milk was present, although in some cases the milk appeared to be more dilute than usual. Histologically the mammary glands of all six were involuting, the alveoli being shrunken, connective tissue increasing, and the gland cells being no longer secretory (see Plate 4, Fig. 2).

This evidence of recent parturition, together with the involution of the mammary glands, strongly suggests that in these cases the calf had been lost at, or very soon after, birth. Yet in five of these six females further oestrous cycles had commenced; in three cases a mature follicle was present, in another ovulation had just occurred, and in the fifth a developing corpus luteum showed that ovulation had recently occurred.

(*d*) *Post-lactational Ovulation*

As shown in Section IV(*b*), lactation in this species continues for approximately $10\frac{1}{2}$ months, most females weaning the calf at the end of June. It has also been shown (Chittleborough 1954) that the majority of mature non-pregnant females experience oestrous cycles during July, August, and September, maturing follicles (pro-oestrus) being most common in July. From this it follows that females do not normally experience a period of anoestrus after lactation. In some cases, as mentioned in Section IV(*b*), oestrous cycles commence during June or early July shortly before lactation has ceased.

VI. Discussion

From the evidence of ovarian activity, near-term foetuses, and new-born calves, the gestation period in the humpback whale occupies nearly 12 months, conception and parturition occurring between June and October, but with maximum frequency of both early in August. Similar results were reported by Matthews (1937), from an analysis of foetal lengths. Conception rarely occurs in the Antarctic; of 250 foetuses taken on the west coast of Australia, only one (4 ft 9 in. long when examined on July 9) could have been conceived in the Antarctic.

The foetal sex ratio is slightly inclined towards males, both for near-term foetuses (51·4 per cent. males) and in earlier stages of pregnancy from the Antarctic (51·9 per cent. males). Higher proportions of male foetuses have been reported from previous Antarctic catches by Mackintosh (1942) (57·4 per cent. males) and Omura (1953) (53·4 per cent. males). As these ratios were based mainly upon smaller foetuses, it might be suggested that a marked excess of males at conception progressively declines during pregnancy so that at birth the sex ratio is only slightly inclined towards males. However, some of the smaller foetuses may have been wrongly sexed. In some of the smaller foetuses the clitoris protrudes quite markedly from the genital groove, and from a brief superficial check can be mistaken for the tip of a penis.

In the humpback whale, ovulation and implantation occur with equal frequency on the left and right sides of the body, unlike the condition in the Odontoceti, where ovulation and pregnancy occur predominantly on the left side (Slijper 1949).

The humpback calf is suckled for approximately $10\frac{1}{2}$ months, lactation being terminated at the end of June in the majority of females. There is no evidence of a sudden increase in baleen growth at the time of weaning (proposed by Matthews

(1937)). As stressed by van Lennep and van Utrecht (1953), weaning is probably a gradual process, the calf suckling less and less frequently as it becomes more independent of the female. Since the calf is not completely weaned until the winter northward migration has taken it away from the Antarctic feeding area, there is no sharp change from a milk to a crustacean diet. A non-feeding period in warmer water (with further growth of baleen) intervenes between weaning and the first season of plankton feeding in the Antarctic.

The composition of the milk is similar to that reported by Clowes (1929), White (1953), Gregory *et al.* (1955), and Ohta *et al.* (1955), for other species of whales and by Pedersen (1952) for the humpback whale.

Previous authors have claimed that the female humpback whale may ovulate, with successful conception, during lactation, but the lack of reliable evidence led Matthews (1937) to reject this theory. Norman and Fraser (1948) state that: "It is believed by one authority that the humpback females become pregnant every year and that pairing takes place again about a month after parturition". Van Lennep and van Utrecht (1953) note that ovulation during lactation is not uncommon in the humpback whale.

Authentic evidence of post-partum ovulation in humpback whales has been slow in accumulating, mainly because females accompanied by calves are protected by international regulation. Evidence must be gleaned over a number of years from the few lactating females which are taken and examined in detail. Conception from a post-partum ovulation results in a female being pregnant and lactating at the same time. However, some whaling inspectors, under the impression that a whale cannot be simultaneously pregnant and lactating, may record the pregnancy but overlook the concurrent lactation.

There is now an increasing amount of reliable evidence that in the humpback whale post-partum ovulation does occur and may result in a further pregnancy while the female is suckling the previous calf. From the Antarctic, Norwegian observers have carefully examined eight female humpbacks which were simultaneously lactating and pregnant, and van Lennep and van Utrecht (1953) have reported another female humpback in the same condition. The evidence from the west coast of Australia is at present confined to one recently ovulated female and its calf which were killed soon after parturition, and three females in both late lactation and advanced pregnancy when killed in June.

It is possible that if more female humpback whales were examined soon after parturition it would be found that post-partum ovulation (followed by lactation anoestrus) is of regular occurrence in this species. It might be argued that if post-partum ovulation occurs regularly, the present investigation on the west coast of Australia should have revealed more cases (in June) of females in both late lactation and advanced pregnancy. Two factors could explain this. In the first place, conception might less often succeed at post-partum ovulation than from oestrous cycles at the end of lactation (as reported by Brambell and Hall (1936) in the lesser shrew). Secondly, pregnant females reach the Australian coast each winter later than most of the non-pregnant mature females, so that by the time the pregnant females reach this area in July and early August, any calves being suckled during pregnancy would

have been weaned. As indicated in Figure 2, very few females in advanced pregnancy are taken on the west coast of Australia during June. Only two pregnant females were examined by the author during June and these were both in late stages of lactation.

Along the west coast of Australia some females lose their calf at or shortly after parturition. Some of these losses may be due to sharks or to killer whales (Chittleborough 1953). It has been shown that in such cases the female recommences oestrous cycles at once. This is similar to the condition in the mouse, where Parkes (1926) found that: "Normal oestrous cycles succeed parturition immediately in the absence of suckling".

If the calf is suckled for the normal period and post-partum ovulation either did not result in pregnancy or did not occur, the female remains in anoestrus until the termination of suckling, at which time (the end of June in most females) oestrous cycles recommence.

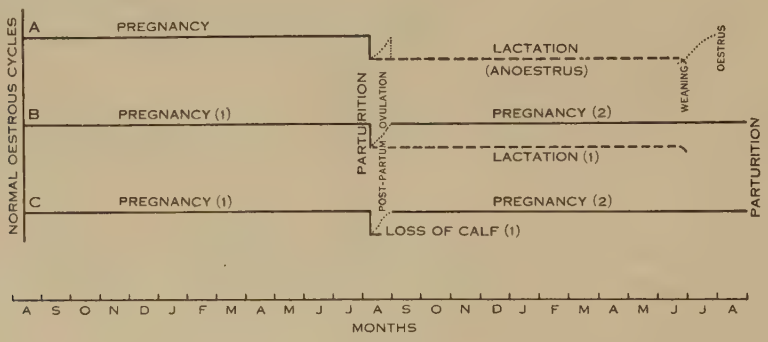

Fig. 4.—Types of breeding cycles found in sexually mature female humpback whales.

Figure 4 summarizes the three types of breeding cycles which have been demonstrated in sexually mature female humpback whales. In the first (Fig. 4*A*), absence of post-partum ovulation, or its occurrence without conception, results in one calf in 2 years. The majority of the breeding cycles in the humpback are of this type. If post-partum ovulation is of regular occurrence, this might help to explain the relatively rapid rate of accumulation of corpora albicantia suggested by some authors (Matthews suggested up to five ovulations in each 2-year breeding cycle).

Figure 4*B* shows a successful post-partum ovulation resulting in two calves in 2 years. Although this type of cycle may commonly occur in female humpback whales it should be noted that this cycle, being slightly longer than that of type A, cannot be maintained continuously by any individual. The post-partum ovulation would occur later (perhaps by a month) each year, progressively lessening the possibility of fertilization. It is probable that after one cycle of type B, a female would revert to a cycle of type A.

In Figure 4*C*, loss of the first calf at or just after parturition is balanced by pregnancy succeeding immediately afterwards. In such cases there would be two pregnancies in 2 years but only one calf reared. This condition is less obvious as it can be diagnosed only within a short period after the first parturition, but it is suggested that it is not uncommon in the humpback whale.

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EXPLANATION OF PLATES 1–5

Plates 1, 3, 4, 5 prepared from sections 7 μ thick, stained with haematoxylin and eosin, using $\times 45$ apochromatic lens, Wratten 11 filter, and microfile film. Magnification in these plates, $\times 640$.

PLATE 1

Fig. 1.—Mammary gland of female in advanced pregnancy. Alveoli well developed, nuclei enlarged and vesicular. No secretion in majority of alveoli, but occasionally a smooth acidophilic secretion (*upper right*).

Fig. 2.—Mammary gland of female in advanced pregnancy. Alveoli well developed, nuclei irregular and darkly staining. Abundant granular basophilic secretion in alveoli.

PLATE 2

Fig. 1.—Ovaries of a female killed shortly after parturition and known to be suckling a calf. Recently functional corpus luteum (95 by 79 by 77 mm, weight 308 g) extending from top of right ovary. Newly formed corpus luteum (59 by 55 by 55 mm) on lower right ovary. Graafian follicles well developed, to 22 mm in diameter, one 34 mm, maturing. (Mammary gland tissue from this female shown in Plate 3, Fig. 1.)

Fig. 2.—Ovaries of a female killed shortly after parturition and considered (but not proven) to be suckling a young calf. Recently functional corpus luteum (104 by 91 by 86 mm, weight 555 g) extending from left ovary. Graafian follicles well developed, to 21 mm in diameter. Histological examination showed that the mammary glands were actively secreting milk.

PLATE 3

Fig. 1.—Actively secreting mammary gland of a female killed shortly after parturition and known to be suckling a young calf.

Fig. 2.—Actively secreting mammary gland of a female in late lactation, killed on June 13. Largest corpus albicans in the ovaries of this female measured 61 by 52 by 48 mm.

PLATE 4

Fig. 1.—Mammary gland of female killed on August 10 soon after weaning the calf in the normal manner. Thick white "milk" (54·5 per cent. fat) present in the ducts, but alveoli regressing and not secretory. Largest corpus albicans measured 49 by 47 mm.

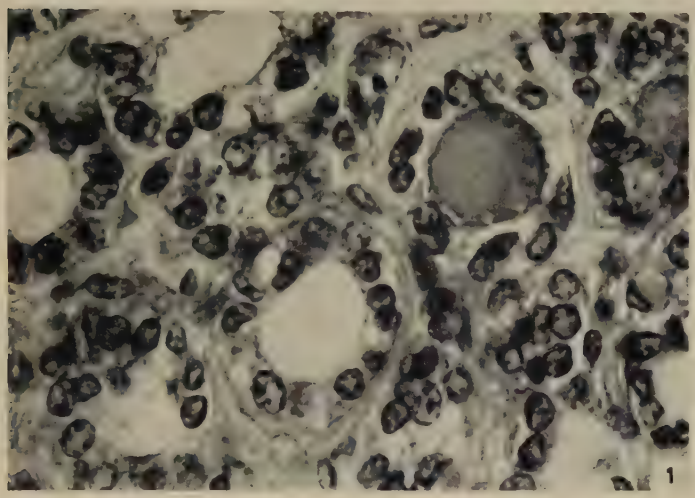
Fig. 2.—Mammary gland of female which had recently given birth but had lost the calf. Rich white milk present in ducts but alveoli resorbing and not secretory. Recently functional corpus luteum (92 by 82 by 77 mm, weight 370 g) hanging from one ovary, and enlarged uteri indicate recent parturition.

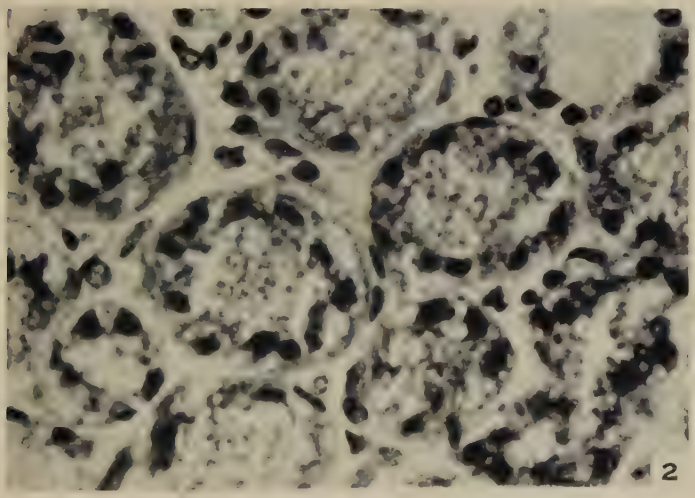
PLATE 5

Fig. 1.—Normal ovum (92 μ diameter) within a 5 mm follicle from an ovary of a female in advanced pregnancy.

Fig. 2.—Fragmenting ovum within an atretic follicle from the same ovary as that of Fig. 1. Note zona pellucida still present but absence of granulosa cells.

BREEDING CYCLE OF FEMALE HUMPBACK WHALE





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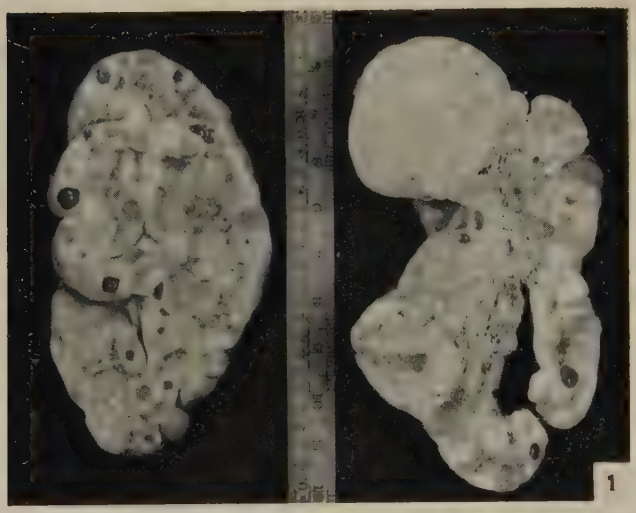

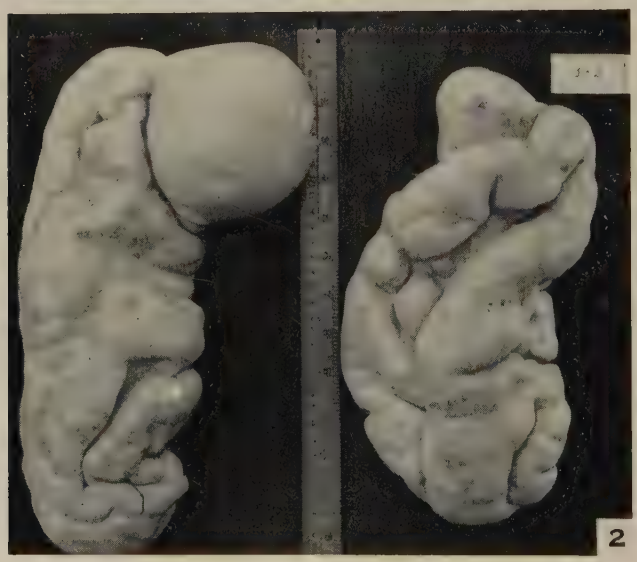

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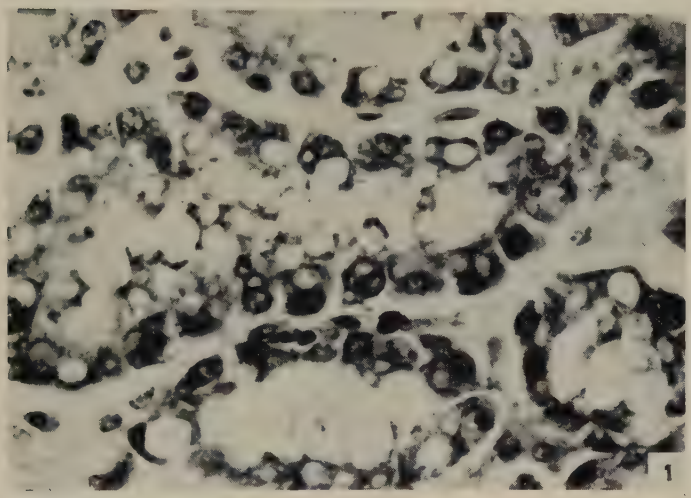

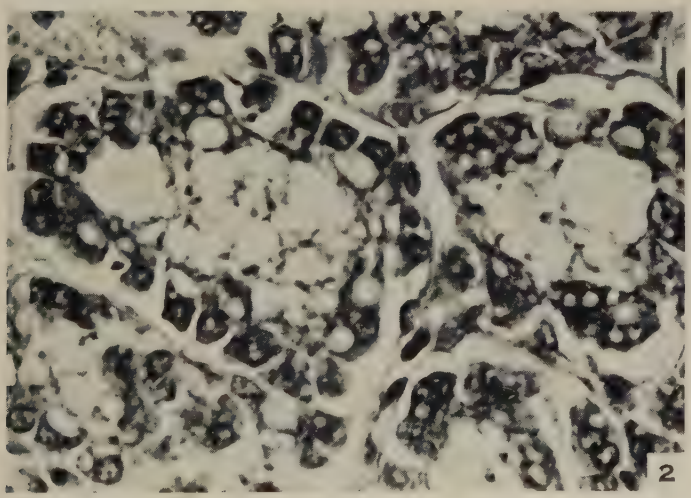

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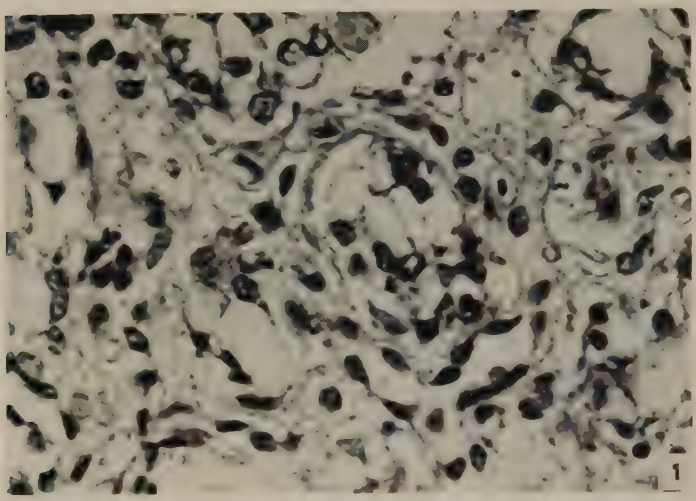
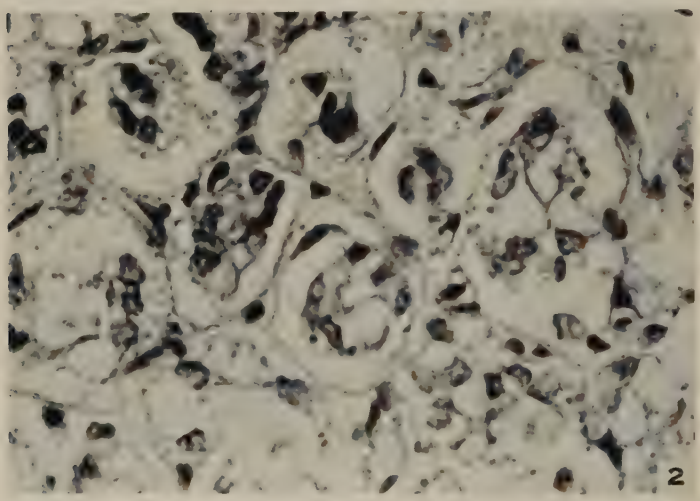
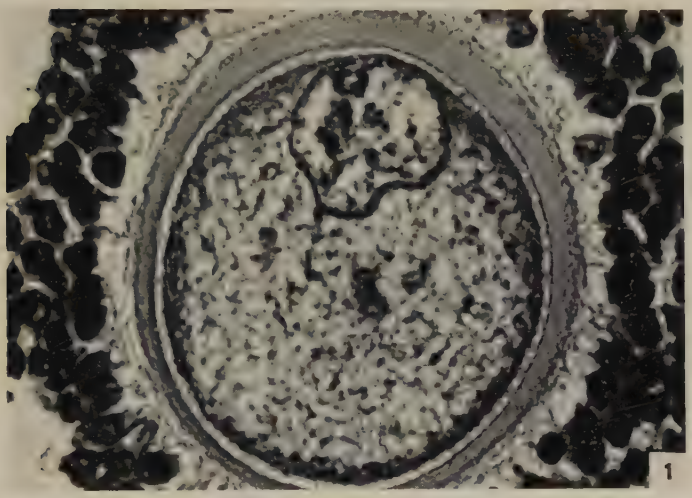
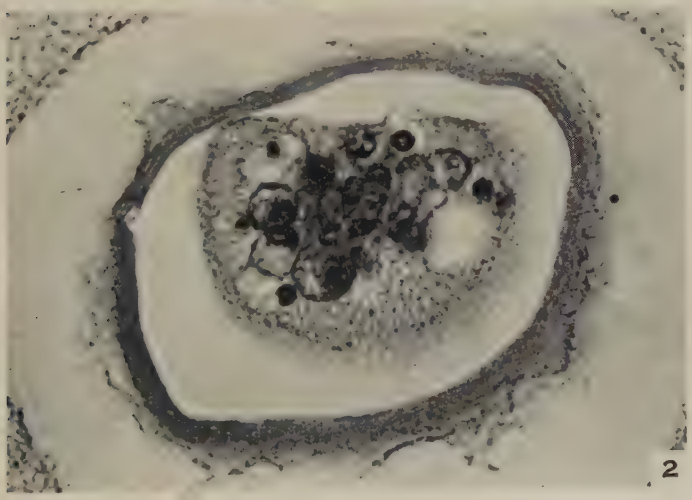




BREEDING CYCLE OF FEMALE HUMPBACK WHALE





THE TASMANIAN TROUT FISHERY

II. THE FISHERY OF THE NORTH-WEST REGION

By A. G. Nicholls*

[*Manuscript received April* 1, 1957]

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Summary

A brief account is given of the several rivers, and of the results derived from the study of the fishery in each. Anglers' returns of catches have been analysed with respect to the daily catch per angler for nine seasons, and the lengths of fish for five seasons, and the results are similar for each river. Detailed consideration of a summary of the data received from all sources in this region shows a definite downward trend in the daily catch which is statistically significant and more pronounced in the estuarine than in the inland fishery. There has been no change in the mean lengths of fish taken, and the size distribution of the catch has remained constant over five seasons. An 80 per cent. annual mortality rate has been found for fish from 1 to 6 years of age, after which it falls slightly. The total annual catch has risen with the increase in licensed anglers. Analysis of the diary of one angler over 27 years shows a decline in the catching rate, but the mean weight of fish has remained fairly constant. No direct consistent correlation was found between the estuarine trout fishery and the commercial whitebait fishery. It is concluded that the decline in catching rate is probably related to a change in the representation of anglers making returns during the nine seasons. A study of the contribution made by the release of hatchery fish shows a maximum possible return to anglers of 2 per cent., subject to a correction for the proportion of takable fish caught by anglers for which no data are available. Evidence is produced to show that the release of hatchery fish is unproductive and wasteful in a stream already stocked to capacity.

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I. Introduction

The North-West Region, an arbitrary division for the purpose of this investigation, includes all those rivers lying to the west of Deloraine. It follows closely the boundaries of the subdivision of the same name as defined in the "Regional Planning Atlas" (Tasmania, Director of Industrial Development 1956), but, of course, includes the whole of the rivers whereas in some cases the upper reaches may lie outside this region as defined in the Atlas. There is, of course, no hard and fast boundary between regions, and anglers resident in any part of the State exercise their right, within the regulations, to fish in any waters they may choose.

In the analysis which follows no reference is made to the Arthur, Pieman, or Montagu Rivers since, although occasional scale samples and reports of catches from these rivers have been received, no body of factual information is available for comparative purposes. In general, with the exception of three or four rivers of the far north-west (west from Smithton), the rivers of this district have much in common. The following facts have been extracted from the Regional Planning Atlas.

Three types of landform are included in this region. The coastal area consists of low plateau, the chief characteristics of which are an altitude range of 300–1500 ft with slopes from 5 to 15°, intersected by steep-sided valleys with slopes up to 35°. It is mostly fertile land and extends along the coast from the eastern boundary to Smithton, varying in depth from 10 to 20 miles. The mean annual rainfall in this area increases from about 35 in. in the east to about 40 in. in the west. Most of the area south of the low plateau consists of high plateau in which the altitude varies from 2000 to 4000 ft, having slopes from 4 to 15°. It is deeply dissected by river gorges with precipitous sides and forms the watershed of the rivers, which all flow in a northerly direction. The rainfall rises to over 70 in. per annum in the mountains. West of Smithton the country is described as plain. It has a depth of 15–30 miles, with an altitude range from sea-level to 600 ft. The rainfall is 40–50 in. per annum.

This region contains one of the main concentrations of population in the State, averaging about 16 persons per sq. mile within 15 miles of the coast.

Some of the more important features of the individual rivers which may influence the fishery are summarized in Appendix I. The most striking feature is the considerable variation in flow, which is likely to cause considerable seasonal fluctuation in the food supply of the fish and may occasionally seriously affect the survival of the young.

The larger rivers open into estuaries of varying extent which provide areas of good feeding and support a tidal water trout fishery. Interest in this is confined to the early part of the season when the whitebait, *Lovettia seali* (Johnston), are running. A commercial fishery of short duration based on this species occurs seasonally.

Complete analyses for most of the river systems of this region have been made separately and the results are available as a Divisional Report (No. 3, 1957). Since in general the results are similar for all rivers, only a survey of the region as a whole is given in detail here. The rivers for which data were obtained are briefly described, in order from west to east, with summaries of the results obtained.

II. The Rivers of the North-West Coast

(a) *The Duck River*

This opens into a semi-estuarine bay at the town of Smithton; it is overgrown for much of its length with willow trees and is subject to periodical flooding. It has numerous tributaries, and good spawning grounds occur in the system. The rather inadequate data indicated a decline in the catching rate over the past few years, in both tidal and fresh waters. Mean lengths of fish caught have not changed significantly over the past five seasons, and the growth rate appeared to be satisfactory.

(b) *The Black River*

This river enters Bass Strait through a good estuary to the east of Circular Head. There are no major towns on the river and the fishery is mainly in the estuary. There was no pronounced decline in the catching rate and no significant change in the mean lengths of fish; growth rate and condition were satisfactory.

(c) *The Inglis River*

This river discharges into an extensive estuary at the town of Wynyard. It has one major and several smaller tributaries, and good spawning grounds occur in the system. A steady decline in the catching rate was found, but the fish lengths have remained constant in both tidal and fresh waters.

(d) *Seabrook Creek*

This small stream opens into Bass Strait 3 miles east of Wynyard. A few scale samples available from this source indicate that the fish become takable by the end of their second year.

(e) *The Cam River*

Flowing into Bass Strait at Somerset, between Wynyard and Burnie, this river has one main tributary and several smaller ones, and falls occur at several places in the system. The catching rate has shown a steady fall, but fish lengths showed no significant change in tidal waters, and a fall in length in fresh waters indicated an increase in fish numbers rather than a decline.

(f) *The Emu River*

The river enters Bass Strait through an estuary 2 miles east of Burnie; falls occur in the system in several of its tributaries. It is possible that there was a decline in the catching rate but the data were inadequate for analysis; there was no change in the mean lengths of fish.

(g) *The Blythe River*

There are several tributaries in this system, which enters the sea about 6 miles east of Burnie. Insufficient information is available for reliable conclusions regarding either rate of catch or size of fish.

(*h*) *The Leven River*

The town of Ulverstone is situated at the mouth of the Leven estuary, into which also flows the Gawler River. The estuary is of considerable extent, some 4 or 5 miles in length and nearly three-quarters of a mile wide in places. It is the centre of an extensive fishery, most productive during the early spring months when the whitebait are running. In the upper reaches of the Leven there is a section about 8 miles in length known as Loongana. This has been stocked for many years with rainbow trout, and was intended as a reserve for that species. Below Loongana the river descends rapidly through a gorge which is probably impassable to fish. In its lower reaches, and in most of the Gawler, are many good stretches suitable for trout and the two are subject to considerable angling pressure. There has been a significant linear downward trend in the daily catch of brown trout from this system over nine seasons, but during the last five there has been no significant change in either the tidal or inland fishery. Examination of the differences in mean lengths of fish showed that they were probably due to sampling errors and not to biological changes in the population. Growth and condition were satisfactory. Information regarding the daily catch for rainbow trout from Loongana was inadequate for analysis, and fish lengths showed differences between seasons but these were not related to the cessation of stocking (Nicholls 1957). Growth and condition suggest that these waters are not ideally suited to rainbow trout.

(*i*) *The Forth River*

This river, which discharges through an estuary about 6 miles east of Ulverstone, has a relatively straight course and is subject to rapid rise and fall of considerable extent. It has one main tributary, the Wilmot River, draining the western side of the basin, and a few smaller ones. Fishing is mainly restricted to the lower third of the basin, corresponding to the region of denser population and better road access. An upward trend in the daily catch was found but the data were inadequate for statistical analysis, and insufficient information was available regarding the size and growth of fish.

(*j*) *The Mersey River*

This is the largest river of the region with several tributaries in some of which falls occur. It opens into a good estuary at Devonport, the principal town in the north-west, and is accessible to anglers at numerous points. Good spawning gravel occurs abundantly throughout the system. A highly significant downward trend in the daily catch was found, but there has been no change in the average length of fish taken from the estuary. There was an increase in the average length of fish from fresh waters but the data were insufficient to disclose the cause.

(*k*) *Port Sorell*

This large estuary receives the waters of three minor rivers, the Rubicon and Franklin Rivers and Muddy Creek, which in some ways are dissimilar from the other rivers of this region. Returns from one angler for six consecutive seasons indicated stability in the fishery of Muddy Creek.

III. The North-West Region

(a) *General*

In this Section the data received from all sources in this region are summarized and considered in more detail. This provides for a reasonably accurate assessment because the conclusions are based on a greater amount of data, and make possible a comparison between this and other regions. It will also be possible to calculate mortality rates; to study the total annual catch per angler; and to attempt to discover the cause of any changes.

(b) *The Daily Catch*

Over the nine seasons under review returns are available from a minimum of eight anglers in 1948–49 to a maximum of 74 in 1952–53. The trends shown in Table 1 indicate that over the past nine seasons there has been a slight but steady decline in the average number of fish taken per angler for each day's fishing in this district.

Table 1

MEAN DAILY CATCH PER ANGLER FOR NORTH-WEST RIVERS

Season	Tidal			Fresh			Combined		
	No. of Fish	No. of Days	Fish per Day	No. of Fish	No. of Days	Fish per Day	No. of Fish	No. of Days	Fish per Day
1945–46	—	—	—	—	—	—	799	241	3·3
1946–47	—	—	—	—	—	—	639	172	3·7
1947–48	—	—	—	—	—	—	513	179	2·9
1948–49	—	—	—	—	—	—	378	108	3·5
1949–50	533	281	1·9	984	287	3·4	1517	568	2·7
1950–51	668	328	2·0	446	156	2·9	1151	507	2·3
1951–52	169	87	1·9	341	117	2·9	638	252	2·5
1952–53	479	260	1·8	918	316	2·9	1464	613	2·4
1953–54	336	218	1·5	888	318	2·8	1224	536	2·3
1945–1954	2185	1174	1·86	3577	1194	3·00	8323	3176	2·62

It is clear that from 1945–46 to 1948–49 the daily catch was well above the mean for the whole period (2·6) and that from 1950–51 to 1953–54 the daily catch lay just below this mean. Although it has fallen from the earlier higher level it appears to be steady at the lower level. Statistically the differences are highly significant.

In tidal waters the daily catch was steady from 1949–50 until 1952–53; in the following season there was a marked drop; this decrease with time is statistically significant. In fresh waters there was a fall from 1949–50 to 1950–51, since when the catch has remained steady with a very slight drop to 1953–54; any differences here are merely of the magnitude of sampling variation and do not indicate a downward trend.

(c) *Fish Lengths*

Over the last five seasons measurements have been made by anglers of a total of 5144 fish from this district: 1765 from tidal waters and 3379 from inland. These are

TABLE 2

MEAN LENGTHS OF FISH FROM NORTH-WEST RIVERS

Season	Tidal		Fresh	
	Number of Fish	Mean Length (in.)	Number of Fish	Mean Length (in.)
1949–50	386	15·6	833	11·9
1950–51	460	15·8	573	11·9
1951–52	248	15·3	364	11·4
1952–53	386	15·4	884	11·5
1953–54	285	15·7	725	11·8
1949–50 to 1953–54	1765	15·6	3379	11·7

set out in Table 2. For tidal waters the differences in the mean length from season to season are not statistically significant and it may be assumed that conditions there

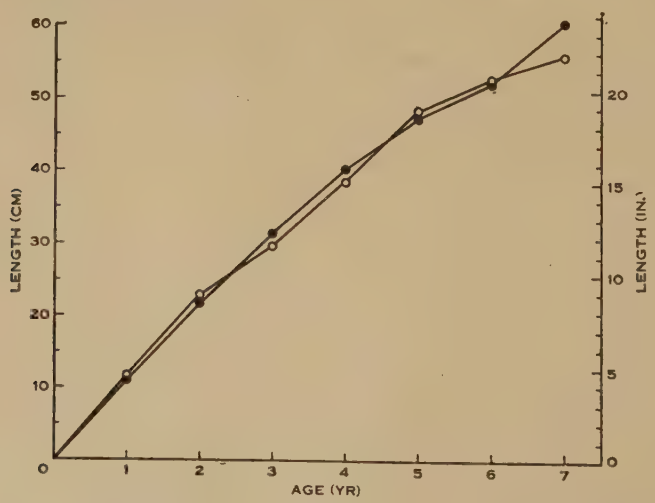

Fig. 1.—Mean length-for-age of fish from all north-west rivers: ● from tidal waters; ○ from fresh waters.

have remained constant. In fresh waters, although the range of variation of the mean lengths is not very large, on examination it proves to be statistically significant. This will be considered in relation to the scale readings.

(*d*) *Growth and Age*

Over the three seasons in which scale samples were collected a total of 846 was taken by anglers; 364 from fish in tidal waters and 482 from fish in the streams. The results of the analyses have been pooled and the grand mean values are plotted in Figure 1, from which it will be seen that the growth in general is very similar in both fresh and tidal waters. This is not surprising since it represents the average growth rate for the whole district and the method of presentation tends to eliminate the differences between rivers. It is of importance, however, in connexion with the study of the

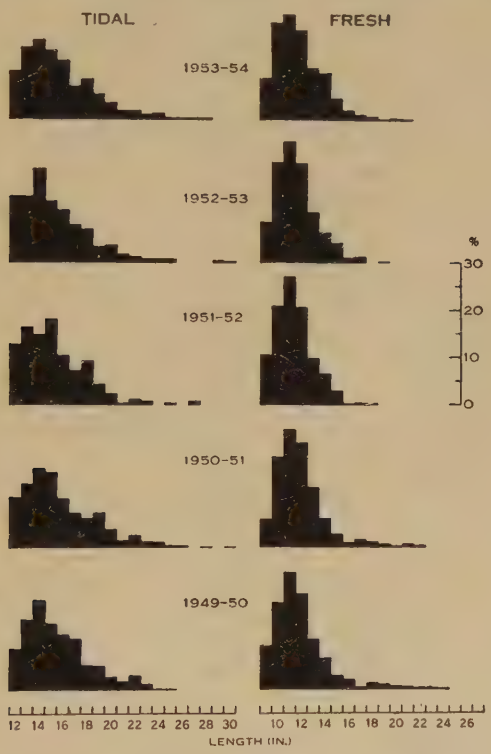

Fig. 2.—Percentage size distribution histograms of length at capture of all fish for tidal and inland waters of north-west rivers.

mortality rates to know that the overall picture of growth is the same in both tidal and fresh waters. The change in growth after the third year, not shown well in this figure but evident in the results for individual rivers, is of considerable interest and is dealt with in Section IV.

When large numbers of fish measurements are available, as in the present case in which figures for all rivers are pooled, it is often possible to discover the age groups represented by means of a percentage size frequency distribution graph, the Peterson method. In Figure 2 this has been done for each season separately using the individual fish lengths which form the basis of the means given in Table 2. In the present case

this treatment does not yield any information as to the different age groups comprising the total population since, as is shown below, the growth of trout covers such a wide range for any given age that there is a very considerable overlap of sizes from one age group to the next. These graphs, however, do serve to show how very constant has been the size composition of the fish caught in each season in both tidal and fresh waters. The values of the mean lengths for each season (Table 2) show how closely they correspond over the five seasons for which there are data. At the same time Figure 2 also shows that there has been practically no change in the proportions of small fish taken.

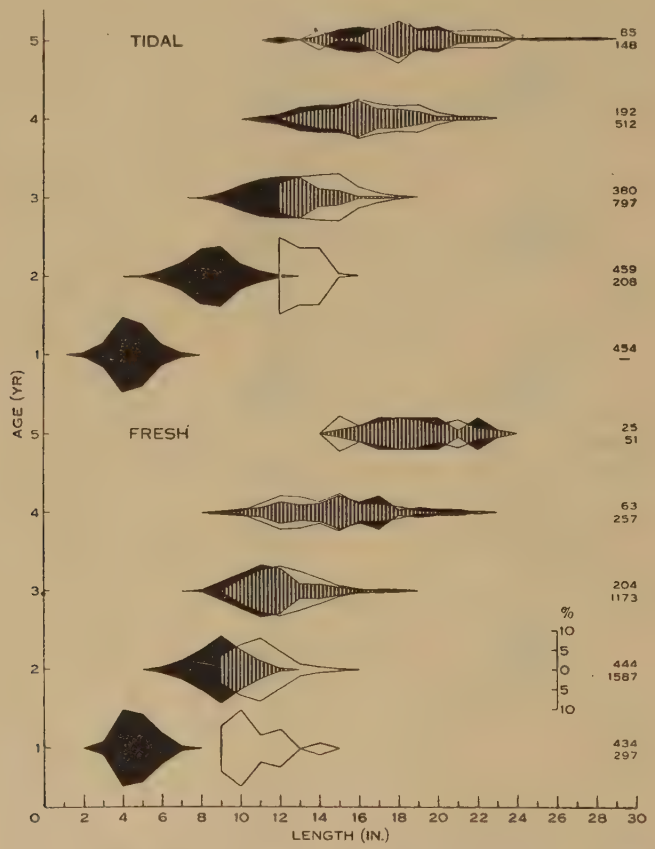

Fig. 3.—Percentage composition within each age group for all fish up to 5 years of age from tidal and fresh waters of all north-west rivers: □ lengths at capture; ■ lengths at end of winter. The numbers of fish are given at the right of the figure, lengths at end of winter above, and lengths at capture below.

From the scales it has been possible to discover the size range at capture of all fish in each age group. By applying these figures to all measurements supplied by anglers these fish can be allocated to their appropriate age groups with a reasonable degree of accuracy. The results are set out graphically in Figure 3, in which is also shown the percentage distribution of the lengths-for-age of all fish whose scales were read within each age group.

Three important facts emerge: firstly, the very considerable variation in the growth rate of fish of the same age, so that as they get older they become spread over a wider range in length. Secondly, this greater spread results in a considerable overlap in size range in fish from several age groups. It can be seen, for example, that the smallest 3-year fish was only 1 in. longer than the largest 1-year fish, and that the smallest 5-year fish (from tidal waters) was the same length as the largest 2-year fish. Thirdly, it is clear that the minimum legal length operates to prevent the capture of large proportions of the first and second year fish in fresh waters and of the second and third year fish in tidal waters. Smaller proportions of even older fish are similarly protected. It will be understood that the size of fish at the end of each winter (shown by the black areas) represents the length of these fish at approximately the same time of the year in each case, and thus represents the size of the fish at the beginning of each angling season. The lengths at capture (shown by the clear areas) naturally represent the lengths of all fish taken during the 9 months of the angling season, which is also the growing season, and will therefore show a greater spread than is actually the case, depending on the time during the season at which they were taken. As the season progresses there will be an increasing number of 1-year fish becoming large enough to be taken, but this will never constitute more than a small proportion of the fish of that age group, and even by the end of their second year a large proportion of the fish will not have attained the legal minimum of 9 in. Almost without exception the largest fish of any age group taken during the season, approached but did not attain the maximum size found for fish at the end of the following winter. (The single exception was in the case of the 1 + fish in fresh water). The histograms of the 1 + fish in fresh waters and the 2 + fish in tidal waters represent only the right-hand "tails" of the corresponding length-for-age histograms, which illustrates the fact that it is the quicker-growing fish of these age groups that become large enough to enter the fishery.

(e) *Mortality Rates*

For fish populations mortality rates can be calculated from "catch curves". This method has been reviewed by Ricker (1948). It involves plotting the logarithms of the numbers of fish of each age group in a catch against the age, and provides a curve of standardized pattern in which the descending right limb is more or less a straight line. The shape of the curve to the left of this line depends on the representation of the age groups so concerned.

In a commercial fishery such as that described by Kennedy (1954) the younger age groups are protected by legal restrictions on the gear, usually by limiting the size of the mesh of the nets. This results in such groups not being adequately represented in the catches, and this portion of the curve must be ignored. In the present case there are minimum legal lengths below which fish must be released, and plotting the figures for each age group by this method yields a curve similar to those shown by Kennedy, except that the descending portion is almost a straight line instead of a slightly convex curve. The significance of this is that the mortality rate for trout in this region, after their third year, is more or less constant. It falls away less steeply after the sixth year.

This method makes possible an assessment of the total population of younger fish by extrapolation of the descending portion of the curve. In order to plot such a curve it is necessary to distribute the total catch into age groups. In the present case

this was not directly possible because scale samples were taken from only a proportion of the fish. But the number of scale readings was sufficiently great to supply information as to the proportion of fish of each length which fell into each age group. From these proportions all fish measured by anglers have been assigned to age groups in order to provide figures large enough to give reliable estimates of mortality. This could have been done for each season separately had there been sufficient data, but because these are too meagre for that purpose the allocation to age groups has been based on the pooled results of all scale readings made from this region during the period.

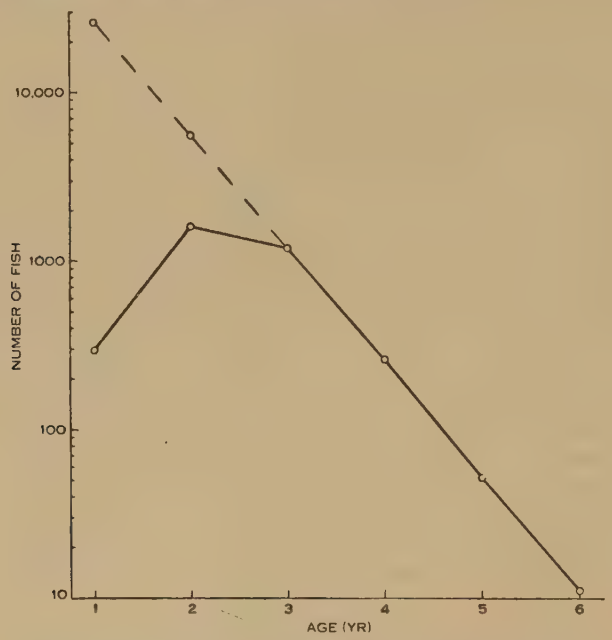

Fig. 4.—Catch curve for inland fishery for 5 years. The extrapolated line indicates about 5500 2-year fish and about 26,000 yearlings.

The result, therefore, may be regarded as an average mortality rate for all rivers of the North-West Region over a period of 5 years. The figures for the number of fish in each age group resulting from this distribution are plotted logarithmically in Figure 4. Figures are available for both tidal and inland waters separately, but since the minimum legal length in the former is higher than in the latter there is a greater amount of data for fish from inland waters. In Figure 4 only the inland water figures have been plotted. Plotting separate curves for each season shows each to be of essentially the same pattern and to have the same slope to the right limb.

The figures show that for the third to sixth years the average mortality rate is about 80 per cent. per annum, and because these points lie on a straight line it may reasonably be assumed that during the second and third years a similar annual rate applies. From the sixth to seventh years the rate falls off slightly to about 70 per cent. These values show such a close correspondence with those worked out by Allen (1951, 1952) during his study of the Horokiwi River in New Zealand that they can be accepted

with confidence. Allen also showed that the rate during the first year of life, ova to yearling, was approximately 99·5 per cent., with the greatest mortality occurring during the first 4 months, in which 97·5 per cent. died. These compare with figures from the United States given by Shetter and Hazzard (1939), and Needham, Moffett, and Slater (1945) quoted by Allen (1951, pp. 100–2).

By extrapolation of the curve given in Figure 4 it may be estimated that the number of 2-year fish should be 5500 as against the 1587 found, which indicates that only 29 per cent. of this group were takable, and that there would have been about 26,000 yearlings as against the 296 (that is, about 1 per cent.) which were large enough to be legally taken. The fact that a proportion of the 2-year fish in fresh water migrate

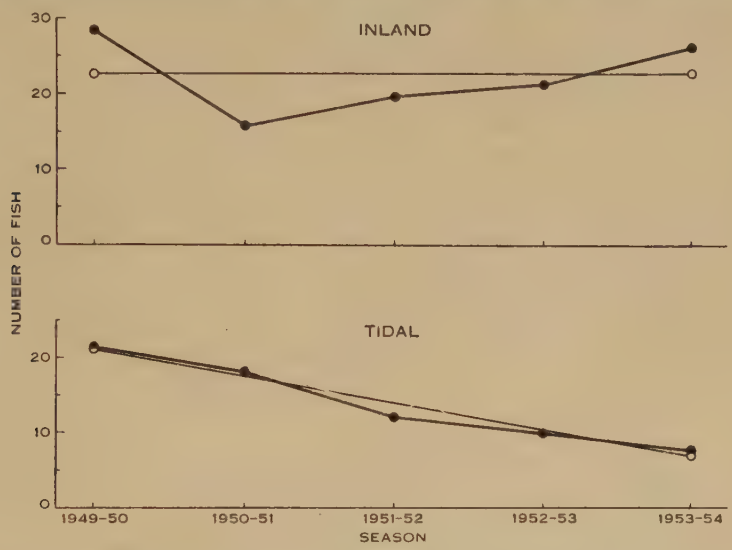

Fig. 5.—Seasonal catch per angler from fresh and tidal waters over five seasons. Regression lines fitted to the points show the direction of the trends.

to the estuary, or even out to sea, does not affect the mortality rates derived from the catch curves since this migration occurs before they reach 3 years. Their presence in tidal waters might be expected to be shown by an increase in the proportions of 2 + and 3 + fish taken there as against those taken inland, but the different minimum legal length for tidal waters completely masks their presence in the estuaries. In any case it is possible that they do not tarry in the estuaries but migrate direct to the sea. This is referred to in Section IV and will be discussed more fully in a later paper.

(*f*) *Seasonal Catch per Angler*

This is the average number of fish taken from all rivers of this district by those anglers who have stated where their fish were taken. It represents any changes more truly than does the daily catch because it is not affected by the omission of days on which no fish were taken. The catches from tidal and inland waters have been examined separately, and the results are shown graphically in Figure 5. It will be seen

that in tidal waters the mean number of fish per angler has fallen steadily over the last five seasons, from 21·3 fish per angler in 1949–50 to 7·7 in 1953–54. The difference between the means is statistically significant at the 1 per cent. level. In the inland fishery, however, although there was a fall from 1949–50 to the next season this was followed by a steady recovery. The difference between the means is not significant and the regression equation indicates a slight upward trend. It may be concluded that there has been no significant change in the inland fishery. These findings support the analysis of the daily catch, which showed similar results.

TABLE 3

ESTIMATED TOTAL ANNUAL CATCH FROM NORTH-WEST RIVERS

Season	No. of Anglers	No. of Fish	Mean Catch per Angler	No. of Licences	Estimated Total Catch	Coeff. of Variation	Standard Error
1945–46	25	1283	51·3	1012	52,000	0·191	10,000
1946–47	21	750	35·7	1063	38,000	0·174	6,500
1947–48	16	595	37·2	1481	55,000	0·213	11,500
1948–49	12	744	62·0	1947	121,000	0·303	36,500
1949–50	47	1702	36·2	2315	84,000	0·127	10,500
1950–51	51	1636	32·1	2772	89,000	0·195	17,500
1951–52	33	1513	45·8	2766	127,000	0·410	52,000
1952–53	88	2676	30·4	2495	76,000	0·171	13,000
1953–54	56	1587	28·3	2562	73,000	0·206	15,000

(*g*) *The Total Annual Catch*

This is based on the average total catch per angler for each season and includes data which it has not been possible to use hitherto, from those anglers who have recorded only their total catches for the season from this district. It is desirable to have an estimate of the total catch for each river separately which would have been based on the average catch per angler (derived from anglers' returns) and the number of anglers fishing each river. However, in many cases there are so few returns from any one river as to cast doubt on the reliability of estimates for these rivers, and in any case figures for the licences issued at each centre are not available.

It has been possible to assess the total seasonal catch for the North-West Region on the basis of similar data for which figures are available. These are summarized in Table 3, in which values are given for the coefficient of variation and for the standard error. It will be seen that there is a considerable range in the probable accuracy of the estimated total catch, so that while, for example, for 1945–46 this is given as 52,000 a figure between 32,000 and 72,000 (differing by up to twice the standard error) would be quite probable. The extent of this range is largely governed by the great variation in the catches by individual anglers which in some years varied from zero to 600 fish.

The figures for mean catch per angler in general show the same trends as the daily catch per angler. But throughout this period, ignoring the high value for 1948–49, it would seem that there has been a steady increase in the total number of fish taken, which reached a maximum in 1951–52 and has since declined somewhat.

IV. Growth in Estuaries

Attention has been drawn to the obvious change in growth rate, usually after the third year but sometimes delayed until the fourth, to be seen in the growth of fish as disclosed by scale readings and illustrated in Figure 6. This change occurs with regularity in fish taken from tidal waters and occasionally in fish taken from above the tidal region. There is no doubt that because of the richer feeding conditions in the estuaries growth is much faster there than in the streams. The difference in growth rate is readily seen on the scales, and with very little practice it is possible to deduce whether a fish has spent any given summer of its life in a stream or an estuary. The better growth in tidal waters is also shown in Figure 3, in which it is evident that the mean length at capture in 3-year fish from tidal waters is larger than in those from fresh waters; for the older fish this is not so clear, for reasons given below.

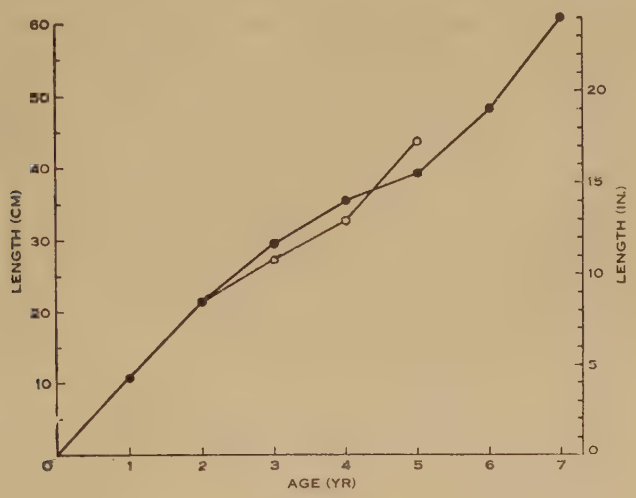

Fig. 6.—Mean length-for-age of fish from: ● tidal, and ○ fresh waters of the Inglis River.

It appears probable that in Tasmanian waters there are two distinct populations of brown trout: one which makes a definite migration to the estuary after the end of the second year while the other remains in the streams. However, members of the stream population may also go to the estuary but this visit is usually delayed until the fish have spawned at least once. Hence the situation arises that the fish taken in the estuaries may have made one or more visits to estuarine waters during the course of their lives, and these visits may occur at any point in their lives. This picture is shown by the scales. Owing to the good growth which occurs in estuaries and because almost all fish make at least one visit to the estuary, there is considerable fluctuation in the growth shown by the population samples from any one estuary. The resulting improved growth rate explains why the growth of fish in tidal waters after the third year may be somewhat irregular, especially when only a small sample of scales is available from any one estuary.

A series of 65 scale samples from the estuary of the Black River was examined to discover the effect of separating the fish into groups according to the year or years in which they visited the estuary. The decision as to whether or not a fish had visited the estuary was made from the appearance of the scales. The length measurements were then made and the fish distributed into groups according to their sojourn in estuarine waters. Fish of all ages were grouped together for this purpose since their age is immaterial and does not affect the conclusions. The results, expressed as the mean length at each year of all fish falling into each group, are shown in Figure 7, in which growth in fresh waters is shown by a continuous line and that in the estuary by a broken line.

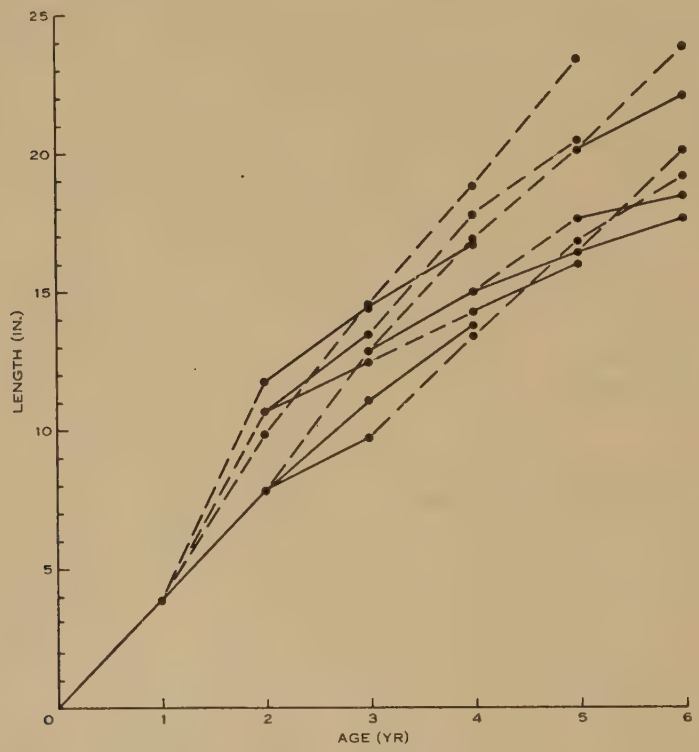

Fig. 7.—Differential growth of trout according to sojourn in fresh or tidal waters: ——— growth in fresh waters; – – – – growth in tidal waters.

The picture is quite clear in the early years but becomes somewhat confused in older fish, partly because fewer fish were available in the 5-year and 6-year groups and partly because the individual variation in growth normally shown by trout tends to obscure the true position when small numbers of fish are being considered. If the fish return to the estuary for several years in succession their growth curves become almost straight lines. These differences become more obvious when two fish of the same age are compared. Of two 4-year-old fish of almost the same length as yearlings, both taken in tidal waters in September, the one which had spent the first 4 years in fresh

water measured 33·0 cm and weighed 710 g, whereas the one which had returned to the estuary annually measured 53·5 cm and weighed 1960 g. The figures represent a 62 per cent. difference in length and a 176 per cent. difference in weight in favour of the fish inhabiting tidal waters. The actual growth curves for both length and weight of four selected individuals are given in Figure 8, and their scales are illustrated in Plate 1.

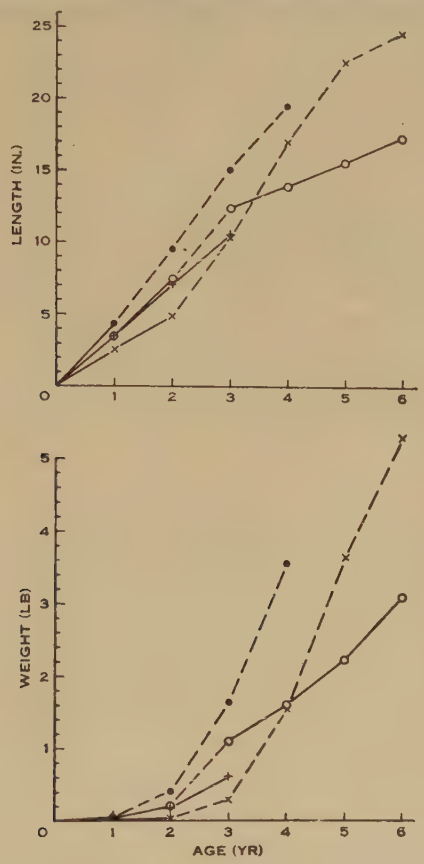

Fig. 8.—Differential growth in respect to length and weight of selected fish according to sojourn in fresh or tidal waters: ——— growth in fresh waters; – – – – growth in tidal waters. Intermediate weights have been back-calculated on the basis of condition factor at capture; this will have led to some inaccuracy but will not have affected the general picture of weight increase. + Three consecutive years in fresh water; ○ 2 years in fresh water, 1 in tidal, followed by 3 in fresh; × 2 years in fresh water followed by 4 in tidal water; ● 1 year in fresh water and 3 years in tidal water.

A comparable condition of improved growth shown on the scales of fish living under conditions of richer feeding can be seen in fish inhabiting lakes which have been enriched by added fertilizers. This has been shown by Smith (1955, Fig. 1*B*) for fish in Crecy Lake, New Brunswick, whose illustration shows the different type of growth particularly well, and by Weatherley and Nicholls (1955, Plate 2, Fig. 3) for fish in Lake Dobson.

It is clear from this analysis that since all of the fish which have been to the estuaries do not necessarily return there every year after spawning, some of them may be taken in fresh waters. This accounts for the apparent discontinuity of growth shown by the scale readings for the older fish from some of the rivers.

Although all the 1-year fish have been regarded as having been reared in fresh water, there is the possibility in cases where they were spawned near the estuary, either in the main stream or in creeks opening directly into the estuary, that some of these fish may have spent the later part of their first year under estuarine conditions.

V. Discussion

The purpose of this investigation was to discover if there was any evidence of deterioration in either quantity or quality of the fish and, if such proved to be the case, to discover the causes and make recommendations for its correction. Arising from the data presented here and as a result of certain steps taken during the course of the investigation, it will be possible to consider also the question as to what contribution to the fishery is made by the release of hatchery-reared fish, and whether such a practice is either necessary or justified. These questions are of major importance in the future administration of the fishery.

(*a*) *Deterioration in Quantity*

There can be little doubt that there has been a falling off in catching rate over the past nine seasons. This has been more pronounced in tidal than in fresh waters. It does not necessarily mean a deterioration in the absolute numbers of fish taken because concurrently with the reduction in the catching rate there has been a steady increase in fishing intensity, as shown by the number of licences issued.

In order to study these factors more closely the data for each river are assembled in Table 4, which shows the mean daily catch per angler for tidal and fresh waters for five seasons, and for each river system for nine seasons. The numbers of licences issued each year in this region are also included. The product of the number of licences and the mean daily catch per angler gives a rough indication of the mean total daily catch for each fishing day in each season. This value has been divided by 1000 and called the "fishing index", and as such it gives additional information on the changes which have taken place in the fishery.

The table shows that fishing in tidal waters through the last five seasons has been at a consistently lower level than that in fresh waters, in the proportion roughly of two fish from tidal waters for every three from fresh. The greatest decline in tidal waters appears to have taken place in the Duck and Inglis estuaries, in which the mean daily catch per angler had dropped in 1953–54 to approximately half the value for 1949–50. The rest show little serious change and with the exception of the Forth River the change has been more or less consistently downwards.

The information available from this analysis extends back only to 1945–46 and it is possible that the daily catch figures over this period represent only the lowest state to which the fishery has fallen after a long period of gradual decline.

Through the kindness of an angler of considerable fishing experience and long residence in the Mersey district, figures for earlier years are available from the diary which he has kept since the 1927–28 season. The daily catch has been calculated from

TABLE 4

DAILY CATCH PER ANGLER FROM NORTH-WEST REGION

River	Tidal					Fresh				
Season:	1949–50	1950–51	1951–52	1952–53	1953–54	1949–50	1950–51	1951–52	1952–53	1953–54
Duck	2·9	2·1	—	1·2	1·3	2·5	1·5	—	—	1·8
Black	1·4	1·9	—	—	1·4	1·0	1·0	—	—	1·0
Inglis	2·3	4·0	—	2·1	1·4	3·6	3·4	—	2·7	2·7
Cam	1·3	1·8	—	1·8	1·2	4·0	2·7	—	3·0	3·9
Emu	1·5	—	—	2·6	1·5	3·7	—	—	1·0	1·3
Blythe	1·6	—	—	—	1·8	4·3	—	—	—	1·0
Leven	2·0	1·5	2·2	2·4	1·4	3·7	2·6	3·3	3·2	3·3
Forth	—	1·7	1·6	1·5	3·8	1·6	5·0	2·2	3·2	2·7
Mersey	1·6	1·9	1·2	1·3	1·4	3·1	3·8	2·7	2·1	1·8
Region	1·9	2·0	1·9	1·8	1·5	3·4	2·9	2·9	2·9	2·8

River	Combined								
Season:	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
Duck	2·3	—	3·0	3·7	2·7	2·1	2·3	1·2	1·5
Black	—	—	—	—	1·4	1·9	1·5	1·3	1·3
Inglis	4·0	4·1	—	—	3·2	3·5	8·3	2·4	2·5
Cam	4·3	5·6	4·0	5·8	3·7	2·4	—	2·6	2·1
Emu	1·0	3·7	3·7	—	2·6	1·3	—	2·3	1·4
Blythe	2·0	2·7	4·8	—	2·4	1·2	—	1·9	1·8
Leven	4·4	3·3	3·3	1·5	2·7	1·8	2·7	2·7	2·5
Forth	5·2	1·0	1·8	2·6	1·6	2·1	2·0	2·8	2·9
Mersey	3·6	3·3	2·5	—	2·4	2·7	1·5	1·6	1·6
Region	3·3	3·7	2·9	3·5	2·7	2·3	2·5	2·4	2·3
No. of licences	1012	1063	1481	1947	2315	2772	2766	2495	2562
Fishing index	3·3	3·9	4·3	6·8	6·3	6·4	6·9	6·0	5·9

this diary in the same way as for anglers' returns in general, except that days with nil catches are included since they have been carefully recorded throughout. This gives a more accurate picture of the fishery in this river, and since it is the result of one angler's

fishing it provides a useful indication of the state of the fishery over a period of 27 years. The data presented in Figure 9 refer only to his fishing in the Mersey River, in tidal and fresh waters, during this period. The mean weights of fish taken are also given since they will indicate any change in the size of fish. In this figure the horizontal lines correspond to the mean weight of fish for each 9-year period. With a view to discovering any trend in the rate of daily catch, curves have been fitted derived from the statistical analysis of the data, in which the peaks, which are mainly due to sampling variation, have been smoothed out.

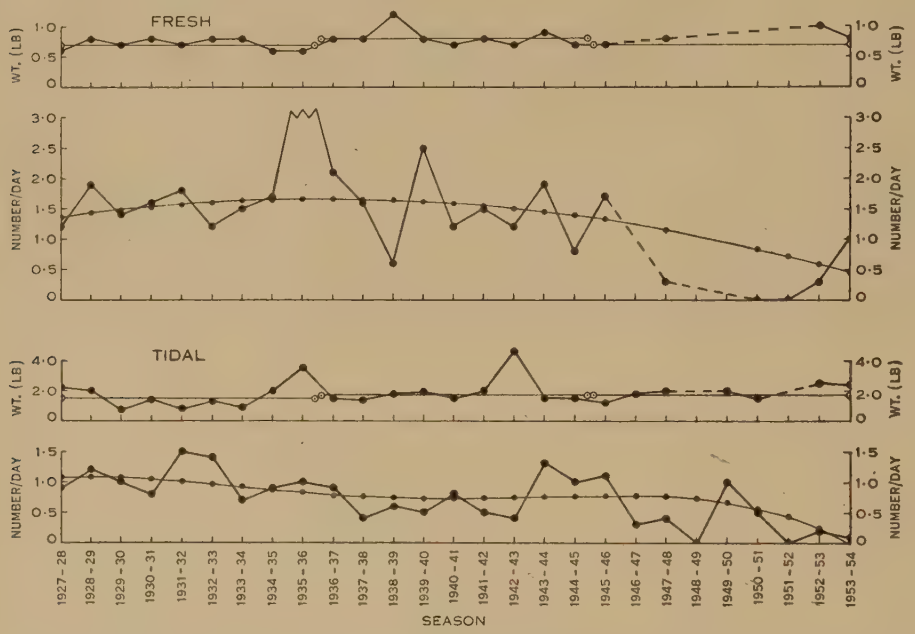

Fig. 9.—Mean daily catch and mean weight of fish taken by one angler from the Mersey River, tidal and fresh waters, over 27 seasons. Horizontal lines superimposed on the weight graphs show the average weight in 9-year periods. The curved lines drawn on the mean daily catch graphs are the result of the mathematical treatment of the data to illustrate the general trends. Broken lines join points between which no data are available for one or more years.

This analysis of the daily catch in tidal waters shows a strong decline which proved to be statistically very highly significant. Over the period of 27 years there is an average linear downward trend in the rate of daily catch, amounting to $\frac{1}{40}$ of a fish per day each season. There was a slight temporary recovery around 1944–45. The average weight of fish has remained very constant.

In fresh waters the analysis shows a downward trend which is not statistically significant. Here, the average linear downward trend in the rate of daily catch amounted to $\frac{1}{65}$ of a fish per day each season. There was a rise to a maximum in 1936–37, followed by an accelerating decline; there is an indication that the decline is greater than the rise, but this is not statistically significant. Again the mean weight of the fish has remained constant.

The apparent considerable fall in mean daily catch in fresh waters was due to "nil" catches in 1950–51 and 1951–52, and to low values in 1947–48 and 1952–53. These values are largely due to reduced fishing activity, for in the two seasons of nil catches only three and one visits respectively were made to fresh waters, and in the two seasons of low catches on only four and six occasions respectively did this angler fish in fresh waters. It would seem, then, that the reduced catches have been in part due to a loss of interest in river fishing, since the number of days spent fishing in each of the three 9-year periods were 172, 131, and 29.

Attention should be drawn to one or two points which may affect the conclusions. Firstly, the values for the 1935–36 season are not reliable since they represent in each case only one day's fishing in tidal and fresh waters. Secondly, a note in the diary indicates that in the 1943–44 season there was an exceptional quantity of whitebait. Although a larger number of fish were taken from tidal waters in this season than in any other, the daily catch figure was not exceptionally high and the mean weight was close to the average, Finally, if the low daily catch values are to be related to a scarcity of fish it would be expected that the fish taken would be above average in weight and length. The figures do not support this, and the data for the Mersey River and those presented in Figure 2 for the North-West Region show that there has been no significant change in length, at least during the last five seasons.

Although there might be an apparent scarcity of fish as revealed by anglers' catches it does not follow that the scarcity was real. The methods of fishing employed by this angler, in common with many others, were consistently the wet and dry fly, with occasional use of the spinner. All of these methods, particularly the first two, tend to be surface fishing, and these three methods are regularly used by anglers fishing for trout when the latter are feeding among the shoals of whitebait which can be seen moving upstream at or near the surface, although they also inhabit the deeper water (Blackburn 1950, p. 187). In years when whitebait are scarce it is to be expected that the trout in the estuary will resort to bottom feeding, and under these conditions the surface and subsurface lures will be less likely to attract fish.

Some consideration should be given to the possibility of variations in the whitebait population having an influence on the catch of trout. Blackburn (1950, Table 11) gives figures for the annual catch of whitebait from the rivers of the north-west coast from 1941 to 1948. The fishery was closed during the following year but the data for later years have been supplied as personal communications, for 1950 by Dr. M. Blackburn and for 1951–1953 by the Fisheries Division of the State Department of Agriculture. The data are shown in Figure 10 for 1943–1953. A better comparison would be obtained by using figures for the catch per scoop. These were given up to 1948 by Blackburn, but he suggested that they might not record changes truly. For subsequent years there is considerable doubt as to the accuracy of the figures for the number of scoops in use.

In comparing the changes in the whitebait fishery with those of the trout fishery there are two lines of argument which must not be confused: (1) that an abundant supply of whitebait would be reflected in an abundance of trout; (2) that a big whitebait fishery would result in a poor trout fishery because of the depletion of their food. These can be examined in relation to the figures for the whitebait fishery and the mean

daily catch of trout extracted from the angler's diary, which are shown in Figure 10. But firstly, it should be noted that at the time when the whitebait fishery was developing (1943–44 to 1945–46) the trout catch was from 1·0 to 1·3 fish per day, and that prior to that, over the preceding 16 seasons during which there was no whitebait fishery, there had been a steady fall in the daily catch of trout (Fig. 9) and that on only two occasions during that period had it exceeded the value for 1943–44. If argument (1) holds there should be a direct correlation between the two sets of figures, whereas if the alternative holds there should be a reverse correlation.

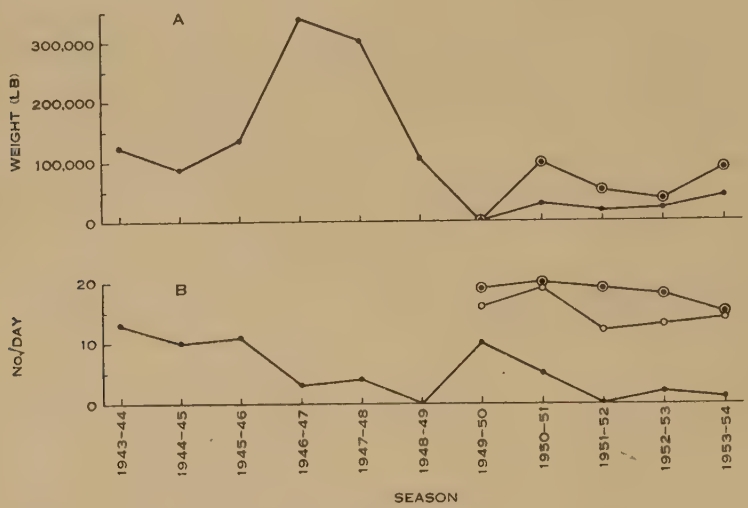

Fig. 10.—*A*, total weight of whitebait taken: ● from the Mersey estuary from 1943 to 1953; ⊙ from all north-west rivers from 1949 to 1953. *B*, mean daily catch of trout: ● for one angler from the Mersey estuary from 1943–44 to 1953–54; ○ for all anglers from the Mersey estuary from 1949–50 to 1953–54; ⊙ for all anglers from all north-west rivers from 1949–50 to 1953–54.

Figure 10 shows that for the first three seasons (1943–44 to 1945–46) and the last four seasons (1950–51 to 1953–54) there was a more or less direct correlation, and that for the two seasons of maximum whitebait catches (1946–47 and 1947–48) there was a reverse correlation, the daily catch of trout falling in 1946–47 with the rise to a maximum in the whitebait fishery and rising slightly the next year with the slight fall in the whitebait catch. This, however, was not continued, as in 1948–49 when the whitebait catch dropped considerably the daily catch of trout fell to zero. The correlation was reversed again in 1949–50 when the whitebait fishery was closed and the daily catch of trout rose to above the average value.

It would be possible to fit an explanation to this apparent lack of correlation along these lines: when there was no disturbance of the whitebait the trout fishery was not affected; the introduction of whitebait fishing did not affect the trout; the sudden rise in intensity in the whitebait fishery caused a drastic upset to the trout, either by direct disturbance, or by the fish feeding on whitebait, or by the elimination of their main food supply so causing them to feed elsewhere; the closure of the white-

bait fishery resulted in a return to normal in the trout catch. But at this point the attempted explanation breaks down, because if the closure of the whitebait fishery in 1949–50 was directly responsible for the improved trout catch of that season it must have been due to a return to normal in the whitebait population, and the figures for the whitebait catches for the following seasons show this to be untrue.

Thus there is no clear evidence that the whitebait fishery has a direct influence on the number of trout taken, though the position is somewhat obscured by the lack of precise information as to the probable total population of whitebait at any one time. To some extent these figures for daily catch of trout are not typical of anglers as a whole, and the data for the whitebait fishery in the Mersey and mean daily catch per angler for all anglers fishing the Mersey during the last five seasons are given separately in Figure 10. These show a maximum catch of trout not in the season when the whitebait fishery was closed, but in the following year, after which there is a decline and subsequent improvement in both. This direct correlation supports argument (1). If, however, the figures for total catch of whitebait along the whole coast be compared with the mean daily catch per angler for the same region (Fig. 10) the reverse correlation holds over the last four seasons, thus supporting argument (2). It is possible, however, that these mean very little, in view of the low figures for whitebait catch during the last five seasons and the absence of figures for tidal fishing for the period prior to the 1949–50 season.

The most probable explanation of the fall in the catch in tidal waters is that in view of the activities of the whitebait fishermen, anglers have formed the opinion that the estuarine fishery has been spoiled, no longer find it attractive, and so pay less frequent visits to tidal waters and naturally catch fewer fish. This viewpoint can be examined by studying the number of visits to tidal waters made by anglers from season to season. The mean number of days' fishing in tidal waters per angler for the whole North-West Region are as follows:

1949–50	1950–51	1951–52	1952–53	1953–54
11·2	10·3	6·7	4·6	5·0

It is clear that there has been a decline in interest in the tidal water fishery over the last five seasons, so that during 1953–54 anglers fished in tidal waters only about one-half as often as they did 4 or 5 years earlier.

It may be concluded that the fall in catch shown in the tidal water fishery is due to a number of causes: a reduced population of whitebait and the greater activity of whitebait fishermen, both of which mean that a greater proportion of trout spend more time at the bottom instead of following the shoals of whitebait, both of which in turn have affected the interest in tidal water fishing and the success of those who depend on surface lures, coupled with an increase in the proportion of less experienced anglers concurrent with the great increase in the number of licence holders. This conclusion receives some support from statements published in the Press from time to time, from one of which the following passage is quoted: "The Mersey yielded more fish—nearly all caught at night and by bottom fishing" (*The Advocate*, June 28, 1954).

As shown in Table 4 there has been a fall in the fishery as a whole over nine seasons, and this was found to be statistically significant. It has also been shown that

the changes in both daily catch and total catch per angler in the tidal water fishery were significant while those in the freshwater fishery were not. From this it may be concluded that any change has been due to the fall in the tidal water fishery.

Reference has been made at the beginning of this Section to the fishing index given in Table 4, which shows changes in the total daily catch from season to season. It will be seen that although the daily rate of catch has fallen, the increasing fishing intensity has resulted in an increase in the number of fish taken. These figures are independent of the extent of fishing, or time spent fishing, since the catch figures represent the means of the actual fish taken per day's fishing. They do not include fishing days on which no fish were taken but, despite a probable increase over the years in the number of fruitless days experienced by the majority of anglers, the fishing index shows a steady rise from 1945–46 to 1947–48, increasing in 1948–49 to twice the 1945–46 value and remaining at a high level during the following seasons, with a slight decline towards the end of the period. This confirms the general picture as shown by the total annual catch discussed above (Section III(*g*)).

It might appear therefore that the fishery is now operating at its maximum level and that the rivers of this region will not carry more than enough fish to give an average of about 2½ fish per day's fishing to about 2500 anglers spending the same amount of time as they have during the past few years. This, however, is not necessarily the true explanation and it is possible that there are other causes for the lowering of the fishing index during the last two seasons.

From the returns of all anglers fishing the north-west rivers during the nine seasons under review it is possible to tabulate the numbers of anglers whose annual catch falls into specified groups. The results are expressed graphically in Figure 11, which illustrates quite clearly the change which has occurred whereby there has been a considerable increase in the numbers of anglers taking smaller catches relative to those taking larger catches.

There are several possible reasons for this: (*a*) there were fewer fish to be taken; (*b*) a greater proportion of anglers recorded zero catches; (*c*) there was an increase in the number of inexperienced anglers.

It has already been shown that there is little evidence in support of there being fewer fish; the second alternative is possible and probably occurred to some extent; but the third appears to be the most likely. Over this period there was a very considerable increase in the number of licences issued, as shown in Figure 11; in 1953–54 there were 2500 licensed anglers as against 1000 in 1945–46. It is a reasonable assumption that the great majority of these anglers were fishing for the first time and lacked experience, so that only small catches could be expected from them. Support for this assumption is provided in the figure, which shows that the maximum number of licences reached in 1950–51 was followed by a slight fall, indicating two or more seasons' experience by the same anglers, and this is correlated with a fall in the percentage of anglers taking 10 or fewer fish and a final rise in the percentages of those taking up to 20 or 30.

It follows that this great increase in the number of inexperienced anglers would undoubtedly affect the figures for daily catch per angler, total catch per angler, and estimated total catch. Thus there is no certainty that the rivers are being fished to

their full capacity as suggested above. Moreover, if this were so, it would be expected that owing to the increased exploitation of the 4+ and older fish the increased mortality among these fish would have shown on the catch curves discussed above, as a tendency to become concave; curves for each season plotted separately showed no such tendency.

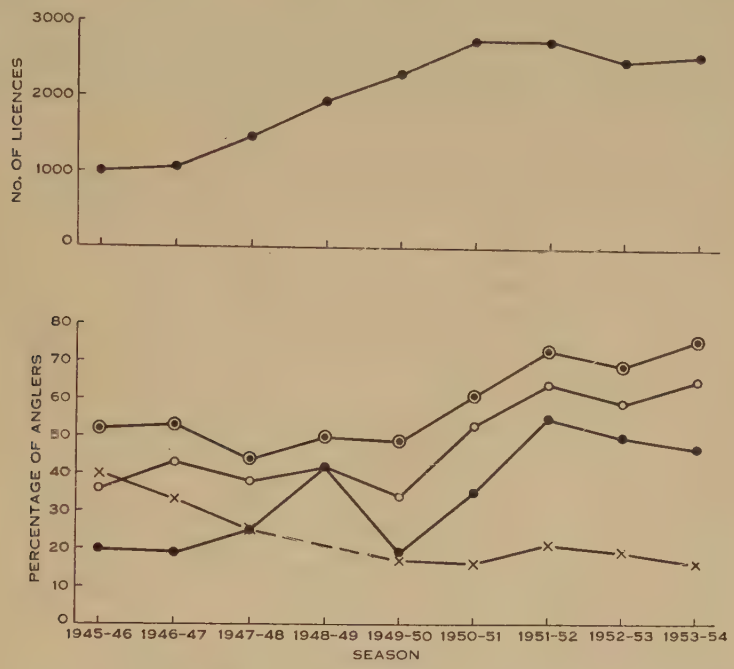

Fig. 11.—Relationship between the number of licences issued and the size of individual catches for all north-west rivers for nine seasons. Percentage of anglers taking: ● up to 10, ○ up to 20, ⊙ up to 30, and × over 50 fish for the season. In 1948–49 very few returns were received and this value is omitted from the last group for simplicity. 1949–50 was the first season for which "nil" catches were recorded by anglers.

If the streams were being fished to capacity it would mean that each season fewer fish would survive to reach a large size, and this would have involved a change in the percentage size distribution shown in Figure 2, whereby the larger fish would have shown increasingly smaller representation. If the trend shown from 1949–50 to 1951–52 of a decrease in representation of larger fish (16–27 in.) in fresh waters had continued through the following seasons, it would have indicated a depletion in the stock of these fish compatible with overfishing, but the fact that the last two seasons show these fish to be represented in increasing proportion indicates that this is no more than a seasonal or sampling variation; moreover the mean lengths of all fish taken would have fallen with time but the figures in Table 2 show that this was not so. At the same time, however, a reduction in the population due to increased exploitation would reduce competition and permit of improved growth; that this has not occurred can be seen from the scale readings.

(*b*) *Deterioration in Quality*

It has been claimed that fish have not been growing as large as in earlier years and that they are in poorer condition. In both cases the complaint probably applies more to lake than to river fish, but it will be considered here briefly under two headings: size of fish and condition.

(i) *Size of Fish.*—Table 2 shows that over the past five seasons there has been no deterioration in size and this need not be discussed further. It will, however, be of interest to compare the lengths of fish from each river in order to discover if there is any variation between rivers.

TABLE 5

MEAN LENGTHS AT CAPTURE OF FISH FROM NORTH-WEST RIVERS

River	Tidal			Fresh		
	Number of Fish	Mean Length (in.)	Standard Error	Number of Fish	Mean Length (in.)	Standard Error
Duck	354	15·4	0·15	109	13·2	0·20
Black	120	18·1	0·26	—	—	—
Inglis	153	14·3	0·23	707	11·5	0·08
Cam	28	15·4	0·53	368	11·8	0·11
Emu	29	13·8	0·52	—	—	—
Blythe	81	15·4	0·31	—	—	—
Leven	561	15·5	0·12	841	11·8	0·07
Forth	128	16·4	0·25	98	11·9	0·21
Mersey	296	15·6	0·16	475	12·3	0·10

For purposes of comparison the means of all fish have been averaged for five seasons within each river, and these figures for tidal and fresh waters are given in Table 5. This shows that in tidal waters the Emu carries the smallest fish (13·8 in.) closely followed by the Inglis (14·3 in.); the difference between these is not significant. The Duck, Cam, Blythe, Leven, and Mersey form a group in which the mean length is about 15·5 in.; the differences within this group are not significant. The Forth comes next (16·4 in.), with the Black River carrying the best estuarine fish averaging 18·1 in.

In the inland waters the Inglis carries the smallest fish (11·5 in.), closely followed by the Cam, Leven, and Forth (with an overall mean of 11·8 in.), while the Mersey (12·3 in.) and Duck (13·2 in.) show the best average size. The differences between the first five named are small, but significant; similarly the difference between the Mersey and Duck is significant.

It would seem therefore that the rivers of this coast vary in their ability to support fish, but before drawing conclusions from this evidence it will be advisable to examine the growth rate for each river as shown by the scale samples. Mean lengths-for-age have been calculated for each river, in both fresh and tidal waters.

The data for fish over 3 years of age are inadequate for a reliable comparison and have therefore been excluded, but it may be assumed that if there is any real difference during the early years it will be maintained during later years.

This comparison has been confined to the four chief rivers from which sufficient information has been obtained, the Duck, Inglis, Leven, and Mersey, and it has been found that there is no significant difference in the mean lengths of fish as between tidal and fresh waters, so that it is justifiable to pool the lengths of fish from these sources in order to obtain a series of means for comparison as between rivers. These pooled mean lengths are set out in Table 6. (The mean lengths at 2 years of age for fish in tidal and fresh waters in the Leven were 22·3 and 23·2 cm respectively, showing a difference significant at the 1 per cent. level.) Statistical analysis of the variation

TABLE 6

MEAN LENGTH-FOR-AGE AND PERCENTAGE INCREMENTS OF FISH FROM FOUR RIVERS

River	L_1		$L_1—L_2$	L_2		$L_2—L_3$	L_3	
	No. of Fish	Mean Length (cm)	Increment (%)	No. of Fish	Mean Length (cm)	Increment (%)	No. of Fish	Mean Length (cm)
Duck	59	11·3	101	60	22·7	35	35	30·6
Inglis	204	11·2	92	205	21·5	34	162	28·8
Leven	430	11·8	93	437	22·8	35	223	30·8
Mersey	58	11·8	82	61	21·5	45	55	31·1
Combined	751	11·6	92	763	22·3	35	475	30·1

between these pooled means shows them to be quite significantly different for all three age groups. It will be seen that the Leven and Mersey Rivers produce better-sized yearlings than do the Duck and Inglis. The percentage increments given in Table 6 show that while growth from first to second years generally decreases from the Duck to the Mersey, the reverse holds during the following year when the best growth is shown by the Mersey fish. No significant difference is found between the Duck and Inglis, nor between the Leven and Mersey, for 1-year-old fish; nor between the Inglis and Mersey for 2-year fish; nor between the Leven and Mersey for 3-year fish.

In a general way this confirms the findings from the study of the lengths at capture of takable fish, but at the same time it is clear that there are no outstanding differences between rivers and that the average lengths of all fish from these rivers at the end of their first three winters are close to 11·6, 22·3, and 30·1 cm respectively. It is probable that a detailed study of growth within any of these river systems would disclose differential growth rates according to where the fish were taken, as was found for the Leven and Gawler Rivers; but insufficient data are available for such a study for all rivers.

(ii) *Condition of Fish.*—In most cases the condition of fish in estuaries differs little from that of fish in inland waters; both tend to be somewhat higher than those of the netted samples (Table 7). It is probable that much of the angling is done towards evening when the fish are feeding whereas the netting was mostly done during daylight, and this might account for a small part of the difference. Netting in the Leven, however, was carried out during the late afternoon and night.

Examination of the values for each season separately shows minor fluctuations within each age group for the three seasons from each source, and no steady decline or improvement. Individual fish within a group show considerable variation. The only trend shown by the condition factor that can be regarded as real is for the younger fish to have a somewhat higher factor than the older fish, though this tendency was not found among fish netted from tidal waters.

TABLE 7

MEAN K VALUES OF FISH FROM NORTH-WEST RIVERS

Age (yr)	Tidal, Anglers'		Fresh, Anglers'		Tidal, Netted	
	No. of Fish	Mean K Value	No. of Fish	Mean K Value	No. of Fish	Mean K Value
7	7	1·16	1	1·09	1	1·10
6	19	1·20	6	1·09	—	—
5	38	1·21	17	1·03	3	1·10
4	107	1·23	37	1·22	16	1·09
3	148	1·22	130	1·26	40	1·08
2	45	1·29	222	1·30	72	1·00
1	—	—	48	1·35	1	1·19

From the somewhat scanty information available for this analysis it can be concluded that there has been no serious loss of condition in trout in this region over the last five seasons. Comparison with values for a New Zealand stream shows that the condition of fish taken from estuarine waters for tagging was similar to that of fish from the Horokiwi River; Allen (1951) also found a slight fall in condition as the fish aged.

(c) *Movements of Tagged Fish*

It was stated earlier (Nicholls 1957) that fish had been netted in estuaries and released after tagging in order to discover if there were any movement of sea-going trout from one river system to another. In addition tagged yearling brown trout were released in the Mersey River and rainbow trout in the Forth and Wilmot Rivers. The results are summarized in Table 8. It will be seen that of the 147 tagged mature fish released in estuaries only five have been recaptured, in each case within the estuary in which they were released; and of the 234 tagged yearlings released in inland waters not one has been recovered.

The number of fish recaptured has been so small that it is not possible to draw conclusions regarding movement of fish from one river to another, but it may be noted that brown trout show a strong homing instinct. This has been demonstrated by the work of the Brown Trout Research Laboratory at Pitlochry in Scotland, where ripe fish transferred from one spawning stream to another have returned to the original stream, which required a preliminary downstream journey against a mass of incoming fish at a time when their spawning urge would involve upstream movement (Matthews 1955). This will be further substantiated in a later paper on work carried out in the Plenty River.

TABLE 8

RELEASES AND RECAPTURES OF TAGGED FISH

River or Estuary	Kind of Trout	Date of Release	Number Released	Number Recaptured	Longest Period of Freedom (days)
Duck	Brown	Sept. 1950	8	1	379
Inglis	Brown	Sept. 1950	84	3	362
Leven	Brown	Sept. 1950	55	1	313
Forth	Rainbow	Sept. 1949	134	0	—
Mersey	Brown	Sept. 1951	100	0	—

(*d*) *The Value of Artificial Propagation*

It was not the purpose of this investigation to consider the question of natural stocking *versus* release from hatcheries. Nevertheless some consideration of this problem is unavoidable especially when, in the light of known mortality rates operating on fish populations, it becomes evident that far more fish are taken by anglers each season than could survive from fish liberated from hatcheries.

Hobbs spent a number of years making a close study of conditions affecting the survival of trout in New Zealand, and his conclusions are summarized in a series of reports (1937, 1940, 1948). He established that except in isolated special cases the artificial propagation of trout in hatcheries is wasteful of effort and funds and makes an insignificant contribution to the fishery (1948, p. 94). In the following pages (95–109) he discussed the findings of similar work in North America and summarized these in the following words: "Revenue arises substantially from the licensing of exploitation of stocks which are produced naturally. It cannot be invested in artificial stocking with the expectation of accomplishing more than small increases in a few places where conditions favour survival exceptionally. This is so, irrespective of the size to which fish are grown before their release" (p. 109).

It is therefore clearly of some importance to the administration of the fishery in Tasmania to know to what extent these findings apply in this State. The question will be considered in the light of available information as it applies to the rivers of the North-West Region, but consideration of the general principle will be deferred to the final report when the whole fishery can be reviewed. When the numbers of

TABLE 9

NUMBERS OF FISH RELEASED AND SURVIVORS, NORTH-WEST RIVERS, 1942–1953

F, fry; Flg, fingerlings; Y, yearlings

Fish Released			Survivors in:											
Year	Number	Stage	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
1942	320,000*	F	—	3,200	640	128	25	5	1					
	13,000	Flg	6,500	1,300	260	52	10	2	—					
1943	374,000	F	—	—	3,740	748	150	30	6	1				
	15,000	Flg	—	7,500	1,500	300	60	12	2	1				
1944	236,000	F	—	—	—	2,360	472	94	19	4	1			
1945	694,000	F	—	—	—	—	6,940	1,388	278	56	11	2	1	
1946	495,000	F	—	—	—	—	—	4,950	990	198	40	8	2	1
1947	372,000	F	—	—	—	—	—	—	3,720	744	148	30	6	1
	79,000	Y	—	—	—	—	—	79,000	15,800	3,160	632	126	25	8
1948	303,000*	F	—	—	—	—	—	—	—	3,030	606	121	24	5
	8,200	Y	—	—	—	—	—	—	8,200	1,640	328	66	13	3
1949	400,000	F	—	—	—	—	—	—	—	—	4,000	800	160	32
1950	890,000	F	—	—	—	—	—	—	—	—	—	8,900	1,780	356
	21,800	Y	—	—	—	—	—	—	—	—	21,800	4,360	872	174
1951	395,000	F	—	—	—	—	—	—	—	—	—	—	3,950	790
	6,600†	Y	—	—	—	—	—	—	—	—	—	6,600	1,320	264
1953	3,000‡	Y	—	—	—	—	—	—	—	—	—	—	—	3,000
		Totals:	6,500	12,000	6,140	3,588	7,657	85,481	29,016	8,834	27,566	21,013	8,153	4,634

*No figures for the actual number of fry released from the Wynyard hatchery are available: the figures given represent the estimated number released based on the number of ova supplied to the hatchery, corrected for normal mortality while in the hatchery.

†Of these, 4000 were marked fish, of which 100 were tagged, released in the Mersey R. at Kimberley.

‡Marked fish; 2000 in the Black R. and 1000 in Sassafras Cr.

fish released from hatcheries over a number of years, the mortality rates, and the total catch taken by anglers are known, it is possible to relate the survival of released fish to the total catch and thus to discover what contribution can be expected from hatchery-reared fish.

(i) *Releases of Brown Trout.*—In the present case figures for releases have been compiled for the records of the Commissioners for a number of years, and the other data have been derived from the analysis of anglers' returns with sufficient accuracy to enable generalized conclusions to be made. The numbers of fish released in all rivers of the North-West Region over a period of 12 years are summarized in Table 9. Fish are released as fry, fingerlings, or yearlings, to each of which a different survival rate will apply. The numbers of survivors from these releases can be assessed by applying known mortality rates, which have been shown to be very similar to those found by Allen in New Zealand, and since he provides figures for survival in quarterly periods it will be possible to apply approximately appropriate rates for each group of fish.

Allen (1952, p. 25) showed that 500,000 fry hatched about October would yield about 4500 survivors by the following July; this represents a 99·1 per cent. mortality from fry to yearlings (taking their age from the time of spawning), or a 1 per cent. survival for fish liberated as fry. Fish liberated as fingerlings from December to May will suffer approximately 50 per cent. mortality; yearlings will be regarded as suffering no mortality for the year of their release. The numbers of survivors calculated on the basis of these figures will be higher than is probably the case. After fish have attained their first year they will be subjected to an 80 per cent. mortality rate annually, leaving 20 per cent. of survivors, except that from the sixth to seventh years a 30 per cent. survival rate will apply. These survival rates have been applied to the numbers of fish released and the results are shown in Table 9.

The catch curves dealt with in Section III(*e*) showed that only about 29 per cent. of the 2-year fish are likely to be taken and only 1 per cent. of the 1-year fish. Table 10 shows the numbers of takable fish surviving from stocking for the last nine seasons, allowing 30 per cent. of 2-year fish and 1 per cent. of 1-year fish to have been takable. The numbers of older fish surviving to the 1945–46, 1946–47, and 1947–48 seasons, which were omitted from this table as a result of ignoring releases prior to 1942, will be negligible.

The estimated total catches made by anglers during these seasons are compared with takable survivors from stocking in Table 10. While these figures may not be very accurate the greatest source of error probably lies in the estimates of total catch. These ratios represent the relationship between the total survivors from stocking and the estimated total catch; they do not represent the contribution made to the total population of takable fish, and could not do so unless all the takable fish were removed from the streams by anglers every year and that this is not so has been shown very clearly. The contribution to the total population of takable fish must be very considerably less, and the contribution to anglers' catches very small indeed.

If the mean ratio over the nine seasons is taken it shows a value of 1 : 51, which means that out of every 51 fish taken by anglers at least 50 were the result of natural spawning, or in other words stocking from hatcheries could not have contributed

more than about 2 per cent. of the total catch. This figure is close to the 3 per cent. return to anglers from the release of marked fish in New Zealand (Hobbs 1948, p. 99), a similarity due to coincidence since the former depended wholly on the rate of stocking. No allowance has been made for the proportion of the population of takable fish removed by angling, for which no information is available for these rivers. If it represents 15 per cent. of the population, the approximate value found by Allen (1951) for the Horokiwi where similar total annual mortalities occur, then it may be assumed that the maximum contribution made to the catches of anglers would be in the region of 0·3 per cent. It will be shown below, moreover, that released fish suffer a higher natural mortality than fish which have been naturally spawned.

TABLE 10

TAKABLE SURVIVORS FROM STOCKING IN RELATION TO TOTAL CATCH

Age (yr)	Takable Survivors in Season:								
	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
7+	—	—	—	—	1	—	—	1	9
6+	—	—	2	3	1	1	2	27	4
5+	—	10	17	6	4	11	134	19	5
4+	52	85	30	19	56	672	96	24	206
3+	428	150	94	278	3358	476	121	1032	620
2+	224	142	416	5037	715	182	1548	930	237
1+	24	69	840	119	30	258	155	40	30
Total	728	456	1399	5462	4165	1600	2056	2073	1111
Total catch	52,000	38,000	55,000	121,000	84,000	89,000	127,000	76,000	73,000
Ratio	1:71	1:83	1:39	1:22	1:20	1:56	1:62	1:37	1:66

In November 1951, stocking the rivers of this region was discontinued in order to determine by actual test whether the populations were dependent on stocking or whether they were self-supporting. By that time the only distributions of brown trout which had been made during that season were 4000 yearlings to the Mersey River and 2600 to the Black River. The hatchery at Wynyard had received 400,000 ova and the 395,000 fry which resulted were released in streams west of the Leven River. Thus the Leven, Forth, and Mersey Rivers received no fish after 1950, apart from the 4000 referred to above. In 1953, 3000 marked fish were released, of which 2000 went to the Black River and 1000 to the Mersey. The last-named contribution is insignificant since only 1 per cent. would enter the fishery during the 1953–54 season. The 4000 fish released in the Mersey in 1951 made only a small potential contribution to the stock, since only 40 would have been takable that season and 220 in the next, and only 160 could be expected to survive to 1954, so that since 1950 these three rivers have received practically no brown trout. In view of this it is of interest to assess the total annual catches from these rivers since the cessation of

stocking, in relation to the survivors existing in each from earlier stocking. In assessing these catches estimates had to be made of the number of anglers fishing each river, since no accurate data were available. It has been assumed that the ratio of anglers sending in returns for any one river to the total number of returns for the region is the same as the ratio of anglers fishing that river to the total number of licenses issued in the North-West Region for any given year. This gives an approximate total catch for each season. In computing the standard errors allowance has been made for the two sources of variation: (1) in computing the mean catch per angler from anglers' returns, and (2) in estimating the proportion of anglers fishing these rivers from the returns. These are given in Table 11, together with the numbers of survivors from stocking.

TABLE 11

ESTIMATED TOTAL CATCH AND FISH AVAILABLE FROM STOCKING FOR LEVEN, FORTH, AND MERSEY RIVERS

Data	Season				
	1949–50	1950–51	1951–52	1952–53	1953–54
(*a*) *Leven River*					
Total catch	22,000	12,500	33,000	14,500	22,000
Standard error	6,500	6,000	15,500	5,000	6,500
Stocking	1,032	231	203	180	70
(*b*) *Forth River*					
Total catch	3,000	3,500	15,000	8,500	8,500
Standard error	1,500	2,500	9,500	4,500	4,000
Stocking	9	72	432	349	102
(*c*) *Mersey River*					
Total catch	9,000	20,000	3,000	15,000	8,000
Standard error	3,500	8,000	1,500	5,500	3,000
Stocking	1,780	415	430	501	242

Although the estimated total catch may have a relatively large variability owing to these two sources of error, in all probability many more fish were taken than could have resulted from those released from the hatcheries. In fact, in the Leven River, more fish were actually recorded as having been taken by the few anglers making returns than were available from stocking. It is also significant that despite the cessation of stocking from 1951 onwards the estimated annual catch in each of these rivers remained relatively high.

Finally, if hatchery-released fish had made any significant contribution to the fishery it would be expected that in the years which followed the cessation of stocking the proportion of young fish would have fallen. Figure 2 shows no significant change

in the shape of the curve among the smaller size groups, and the percentage of fish in the 1+ and 2+ age groups showed little or no change over the five seasons. The percentage figures for 2+ fish in tidal waters for the five seasons were 11·1, 11·1, 12·5, 13·0, and 11·2; and for the 1+ and 2+ fish in fresh waters the figures were respectively: 8·6 and 46·2; 8·0 and 45·5; 9·3 and 50·3; 9·0 and 48·3; and 8·8 and 45·7.

(ii) *Releases of Rainbow Trout.*—Reference has been made to that section of the Leven River known as Loongana which has been stocked with rainbow trout only. In addition there has been a concerted effort over a number of years to stock the Forth River with this fish, since this river appeared to have characteristics suited to the species. The rivers are dealt with separately.

(1) *The Leven River at Loongana.*—Figures for releases, survivors, and numbers of takable fish surviving are available but it is almost impossible to assess with any degree of accuracy the total catch from this source, since few returns refer to fishing in this section of the river. However, scale samples from 116 fish taken at Loongana between November 30, 1952, and March 21, 1953, showed that 5 fish (4·3 per cent.) were 3 years old; 25 fish (21·6 per cent.) were 2 years old; and the remaining 86 (74·1 per cent.) were yearlings. The last release at that point was of yearlings in 1951 and these fish would have been 2+ fish in the 1952–53 season, from which it follows that all of the yearlings taken in that season, nearly 75 per cent. of the total catch, were spawned naturally. The daily catch figures showed no serious decline in the fishery at Loongana subsequent to the cessation of stocking, and it would appear that rainbow trout are self-supporting in the upper reaches of the Leven River. An analysis of the lengths of fish taken from Loongana shows that there is no reason to doubt that the stock remained fairly constant subsequent to the cessation of stocking, in view of the absence of any significant trend in the size of the fish. If this is so it can only be concluded that previous stocking was ineffective and therefore unnecessary, since if there had been any real contribution from this source the mean lengths should have increased after stocking ceased.

(2) *The Forth River.*—In an effort to stock the Forth River with rainbow trout the Commissioners decided to release yearlings in considerable quantities in the lower reaches above tidal waters. It was anticipated that the fish would become accustomed to estuarine conditions and remain there, as previous experience of releasing this species in rivers had suggested that the fish had gone to sea and not returned.

This policy was put into effect in 1948 with the release of 22,000 yearlings; it was to be followed by an annual release over the next four years but this was discontinued after the 1951 release in conformity with the decision to cease stocking these rivers. It was in any case becoming apparent that the policy was not likely to prove successful since very few of these fish were taken by anglers. A possible reason for the failure can be seen from Table 12, which sets out the releases and probable survival of these fish, based on the mortality rates used for brown trout. It is clear that the population becomes very rapidly reduced in numbers when an annual mortality rate of 80 per cent. applies, and it is also possible that yearling fish released in or near tidal waters suffer a mortality rate very much higher than normal owing

to the lack of protection and the presence of predators. However, the main point of interest here is that of the 734 fish recorded by anglers as having been taken from the Forth River from 1949–50 to 1953–54, only 8 were rainbow trout. It would thus appear that in spite of the fact that over the past 6 years 43,000 rainbow yearlings have been released as against only 8000 brown yearlings, browns outnumber rainbows by nearly 100 to 1.

TABLE 12

RELEASES AND SURVIVAL OF RAINBOW TROUT IN THE FORTH RIVER

Year of Release	Number Released	Age (yr)	Numbers Surviving in Each Year					
			1948	1949	1950	1951	1952	1953
1948	22,040	1	22,040	4,408	882	176	35	7
1949	6,650	1	—	6,650	1,330	266	53	11
1950	5,400	1	—	—	5,400	1,080	216	43
1951	9,500	1	—	—	—	9,500	1,900	380
Total	43,590		22,040	11,058	7,612	11,022	2,204	441
Takable			—	—	1,308	839	836	441

(iii) *Recovery of Marked Fish.*—Table 13 shows the releases of marked fish in the rivers of the North-West Region since 1949. Only one of these fish has been reported as having been taken.

TABLE 13

RELEASES OF MARKED YEARLING FISH IN NORTH-WEST RIVERS

Date of Release	Kind of Fish	Numbers of Fish			Place of Release
		Marked	Tagged	Total	
Sept. 1949	Rainbow	773	134	907	Forth R.: above tidal waters to Wilmot junction
Sept. 1951	Brown	3900	100	4000	Mersey R.: Kimberley
Aug. 1953	Brown	2000	—	2000	Black R.: Mawbanna
	Brown	1000	—	1000	Sassafras Creek:* Mole Creek
	Rainbow	511	—	511	Ration Tree Creek:* Liena
Sept. 1954	Rainbow	2500	—	2500	Blythe R.: Upper Natone

*Sassafras Creek and Ration Tree Creek are tributaries of the middle reaches of the Mersey River, near Mole Creek and Liena respectively.

At normal survival rates there should have been 69 takable fish in 1951–52, of which 6 should have had tags; in 1952–53 there should have been 240, with 7 tagged fish; in 1953–54 there should have been 192 (5 tagged); and in the two subsequent

seasons 267 and 296 takable survivors respectively. Publicity may have been inadequate, for it was not until the 1952–53 season that this was included on the licence, although printed notices were widely distributed in December 1951, at which time yearlings released in 1949 would have been 3 + fish and of takable size. It is possible that marked fish were overlooked and also that some tagged fish were taken illegally and so not reported.

No conclusive results can be derived from these rather limited releases other than support for the statement made above, that this method is of little value unless conditions are such that the population can be adequately sampled by reliable means. Fishing by electricity makes this possible. A D.C. generator producing 5 A at 200 V, of similar design to that described by Hammond-Davies (1952), has been assembled. It is unusual to get more than 2·5 A from this machine in Tasmanian waters where the mineral content is very low (about 40 p.p.m. total dissolved solids) and the usual output is less than 1 A. Nevertheless it has been found to work very satisfactorily under these conditions and fish of all sizes are readily caught.

TABLE 14

RESULTS OF ELECTRO-FISHING IN TWO STREAMS

Stream	Site	Distance Fished (yd)	Area Fished (sq. yd)	Number of Trout Taken	Weight of Trout lb	Weight of Trout oz	Number of Trout per mile	Number of Trout per acre	Weight of Trout per acre (lb)
Ration Tree Creek	—	104·0	496	64	4	14¼	1083	625	47·7
Sassafras Creek	I	129·3	578	104	21	6¾	1415	871	179·4
Sassafras Creek	II	94·0	402	48	8	4¼	899	578	99·5

In practice a section of stream is selected such that the truck carrying the equipment can be brought alongside. The negative electrode, a floating screen 3 by 2 ft, is placed in the stream at that point; stop nets are set at the upper and lower limits reached with the available cable, and the stream is then worked, with the positive electrode carried by one man and the fish collected in a dip-net carried by a second. A third man, when available, is employed in keeping the cable free from entanglements and carrying the fish back to a central holding box. The section of stream is measured along the centre of its bed, and the width, and depth at the centre, are measured at 18-ft intervals in order to obtain mean values for calculating the area and cross section.

Two streams in which marked fish were released in 1953 were visited with this equipment in April 1955. Ration Tree Creek could be worked at one site only, corresponding to the position at which the fish were released; Sassafras Creek was worked in two places: the position of release of the fish and about 1½ miles above. The relevant data are summarized in Table 14.

(1) *Ration Tree Creek.*—In this stream, in addition to the brown trout, 1 blackfish (*Gadopsis marmoratus* Richardson) and 12 eels (*Anguilla australis* Richardson) were taken. These numbers represent 17 blackfish and 203 eels per mile of stream, and would add 20·7 lb to the weight of the standing crop, giving a total of 68·4 lb per acre. The scales taken from the 64 fish caught here yielded information as to age and growth which is given in Table 15. These showed that the period of summer growth was over, and the majority had several rings of winter growth at the edge.

TABLE 15

MEAN LENGTH-FOR-AGE OF TROUT FROM RATION TREE CREEK

Year Class	Age (yr)	Number of Fish	Mean Lengths (cm)		At Capture		
			L_1	L_2	Length (cm)	Weight (g)	K Value
1952	2+	1	9·5	16·0	22·0	175	1·64
1953	1+	14	10·6		19·5	95	1·26
1954	0+	49			10·4	14·5	1·29
Grand mean			10·5	16·0	—	—	1·29
Increment (%)			52·4				

The proportion in which each age group was represented in the population indicates a 71 per cent. mortality rate in fish nearly 1 year old to those nearly 2 years old, and 93 per cent. in fish a year older. This sample, containing only one 2+ fish, is probably not truly representative of the whole population, and the mortality rates are of only limited application. The most interesting fact was the occurrence of large numbers of fish still in their first year. This suggests that the area is one of successful spawning and the stream may be regarded as a typical "nursery" stream, producing young fish which will migrate downstream, but not able to carry many older fish.

The standing crop of nearly 48 lb per acre for trout is not high, owing to the fact that the population was mainly fish less than 1 year old; but the total crop of all fish, 68 lb per acre, shows that the stream is reasonably productive. None of the fish was of takable size.

(2) *Sassafras Creek.*—This stream was more accessible than Ration Tree Creek and was worked at two positions about 1½ miles apart. No fish other than trout were found here. The figures for the two sites can be combined, and show that for these sections of this stream the population was 1198 fish per mile of stream, or 751 per acre; 18 per cent. were above the minimum legal length. The figure for the standing crop was 146·6 lb per acre, indicating that the stream is highly productive.

The scales from these fish, particularly those from site I which was in a public reserve, contained a large proportion of replacement scales, especially among the larger fish. In some cases no readable scales were found and these fish are perforce omitted from the age and growth data. This condition suggests that the stream is extensively fished at the more accessible points and that the majority of fish have been caught and returned, probably more than once.

Length and weight measurements and scales were obtained from a random sample of 50 fish over 10 cm and from 9 smaller fish, at site I; all fish from site II were examined. The remaining 45 fish at site I were weighed in bulk and had an average weight not very different from those of the random sample (3·2 and 3·9 oz respectively). Scale readings are available from 100 fish and the results are given in Table 16. Statistical tests of the lengths-for-age and lengths at capture of fish from both sites show that there is no significant difference, and the results have therefore been pooled. Comparing these figures with those in Table 15 shows that at capture, fish in their first and second years were larger in Ration Tree Creek than in Sassafras Creek.

TABLE 16

MEAN LENGTH-FOR-AGE OF TROUT FROM SASSAFRAS CREEK

Year Class	Age (yr)	Number of Fish	Mean Lengths (cm)			At Capture		
			L_1	L_2	L_3	Length (cm)	Weight (g)	K Value
1951	3+	4	8·6	21·4	26·4	29·3	253	1·00
1952	2+	22	8·3	18·0		21·8	121	1·15
1953	1+	59	8·6			18·2	75	1·20
1954	0+	15				8·2	7·5	1·36
Grand mean			8·5	18·5	26·4	—	—	1·18
Increment (%)			117·6	42·7				

Mortality rates in Sassafras Creek were 63 per cent. for fish from nearly 2 years old to nearly 3, and 82 per cent. for fish from nearly 3 years old to nearly 4. These are subject to a correction for six of the larger fish whose scales were unreadable and which it was impossible to allocate to their probable age groups with any degree of accuracy. The absence of a large proportion of fish in their first year is an interesting feature which recurs in similar work in other streams. It suggests that where spawning occurs in a stream already inhabited by older fish, which has been shown to occur by Allen (1951, p. 77 *et seq.*), the mortality of the young fish is very heavy. Fish were earlier seen spawning in Sassafras Creek at site I. This supports the idea that the main recruitment to stocks comes from small streams, such as Ration Tree Creek, not inhabited by many older fish. The average depth of this creek was 7·4 in. whereas that of Sassafras Creek was 13·3 in.

Of the 1511 marked yearlings released in these two streams in August 1953, not one was found 20 months later. These fish would have been nearly 3 years of age, and from Allen's (1952, p. 25) mortality rates there should have been about 70 2+ marked fish in Ration Tree Creek and about 140 similar fish in Sassafras Creek. Of 106 fish in the latter, 22 were 2+, 4 were 3+, and 6 whose scales were unreadable were almost certainly at least 2+; thus it is reasonable to assume that of the 152 fish taken in that section of the stream 46 were 2+ or more, and at least 32 were 2+. This stream could obviously support fish of nearly 4 years of age, since at least 4 per cent. were fish of that age.

The situation in Ration Tree Creek is not so clear, since the released fish were rainbow trout, and little is known about the behaviour of these fish in Tasmanian streams other than that nearly all attempts to stock rivers with this species appear to have failed. In the past it has been assumed that these fish are strongly migratory in their habits and that all have gone to sea and not returned. The exception to this general rule is that section of the upper Leven River, at Loongana, which is cut off from the lower reaches by an impassable gorge. The fact that the fish there continue to maintain themselves without restocking shows that it is not essential to their well-being that they should migrate to sea, and it is possible that the explanation of previous failures is that the stocking rate was not sufficiently high in relation to the existing population to enable them to become established.

It is probable that survivors of the rainbow trout released in Ration Tree Creek in August 1953 would have moved downstream before April 1955 in any case, as they would then have been nearly 3 years old and this creek was carrying only very few fish at that age. This possibility is supported by the capture on December 2, 1956, from the Mersey River near Mole Creek of a rainbow trout corresponding in age and mark to the released fish. This bears out the supposition that they do not necessarily migrate to sea.

The upper reaches of the Blythe River were also stocked with rainbow trout in September 1954, and an attempt was made to fish this section of the stream with the electric equipment. Conditions at the time made this impossible. A large-scale experiment on stocking with marked fish is at present being conducted in the North Esk River, and the results will be presented in due course.

The results given above serve only to emphasize the futility of releasing fingerlings in streams already inhabited by older fish. Evidence is available that released fish are eaten: a partially digested tagged fish has been recovered from inside a larger fish. It seems self-evident that where a stream is inhabited with a normal population from natural stocking, which there is every reason to believe will be up to the capacity of the stream, the introduction of thousands of hatchery-reared fish all at once gives them very small chances of survival. Available shelter is already occupied, the newcomers are strange to the surroundings and unused to foraging for themselves, and so serve only as a valuable short-term supplement to the food supply of the residents.

Efforts to evaluate the survival of hatchery-reared fish after release have been made on many occasions in North America. Schuck (1948), reviewing some of

this work, gives figures which show that of nearly 27,000 brook and rainbow fingerlings, from 3·5 to 4·0 in., only 147 (0·54 per cent.) were recaptured by anglers, and for larger fish, 4·0 to 6·0 in., of 7400 released only 245 were recaptured (3·3 per cent.). (The overall contribution to the fishery of these 34,000 fish was 1·1 per cent.)

He pointed out that the extremely low return to anglers was due to a low survival rather than to "ineffective angling removals", and that survival was much poorer than that of naturally spawned fish of the same age. In one particular case of brown trout, over a period of 1 year there was a 6·3 per cent. survival of hatchery-reared fish as against a 23 per cent. survival of naturally spawned fish.

VI. Acknowledgments

Help received from official sources has been acknowledged in Part I of this series. The anglers who sent in returns of their catches during the nine seasons on which this report has been based are too numerous to mention individually, although they constitute such a small percentage of licensed anglers. Their contribution to this investigation is appreciated. Special thanks are due to the numerous anglers who sent in field record books recording their captures and taking scale samples. I am greatly indebted to Mr. S. S. B. Purves for allowing me to study his angling diary which he has kept since 1927–28, and to publish the results of the analysis here.

The statistical analyses of the daily catch per angler data have been carried out wholly by the Division of Mathematical Statistics, C.S.I.R.O., and it is a pleasure to acknowledge the help received in this connexion from Dr. A. T. James of that Division, and also for his analysis of the data derived from the angler's diary. In the remaining statistical work assistance was given by Mr. P. Sprent, Department of Mathematics, University of Tasmania, to whom also thanks are due. Thanks are also due to those who have read the manuscript, and especially to Mr. K. R. Allen whose comments, based on many years' experience with this type of work in New Zealand, have been most helpful and greatly appreciated.

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THE TASMANIAN TROUT FISHERY. II

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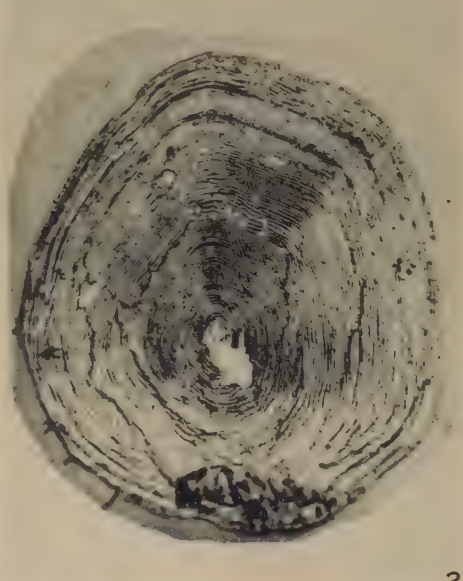

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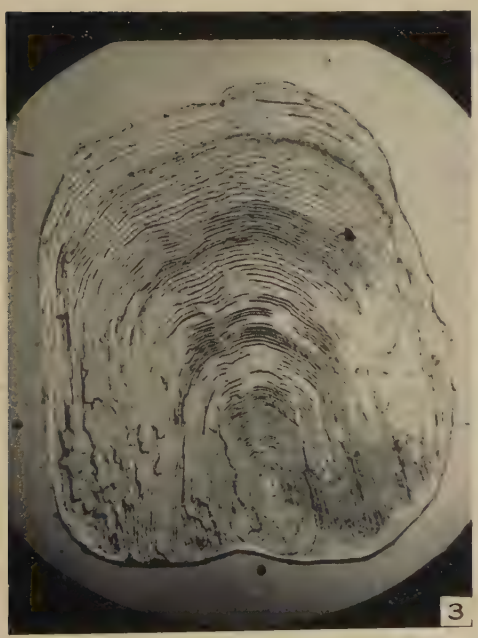

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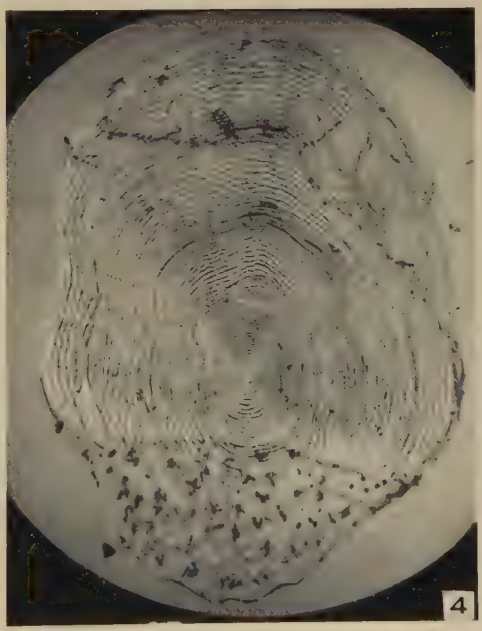

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EXPLANATION OF PLATE 1

Scales from four brown trout taken from the Black River estuary, showing the differences in growth rate which occur when the fish spend their growing season in fresh waters or in tidal waters. The magnification of these scales was not constant.

Fig. 1.—Scale from a female fish showing 3 years of inland growth. This fish was 3 years and 5 months old when captured; it measured 13 in. and weighed 1 lb 2 oz. Winter rings end at about 3½, 7, and 10½ in., followed by nearly 2½ in. of growth since it went to the estuary (ref. 50/51, 36·1).

Fig. 2.—Scale from a male fish showing 2 years of inland growth, 1 year in tidal waters, followed by 3 years during which it appears to have remained inland. This fish was 6 years and 3 months old when captured; it measured 18¼ in. and weighed 3 lb 8 oz. Winter rings end at about 3½, 7½, 12½, 14, 15¾, and 17½ in. It had made about ¾ in. of growth since returning to the estuary in its seventh year (ref. 50/51, 35·13).

Fig. 3.—Scale from a male fish showing 2 years of growth in the stream followed by 4 years in tidal waters. The fish was 6 years and 4 months old when captured; it measured 26 in. and weighed 5 lb 7 oz. Winter rings end at about 2½, 5, 10½, 17, 22¾, and 25¾ in. and it had made only ¼ in. of growth since returning to the estuary in its seventh year (ref. 50/51, 35·27).

Fig. 4.—Scale from a male fish showing 1 year in fresh water followed by 3 years under estuarine conditions. The fish was 4 years and 3 months old when captured; it measured 21 in. and weighed 4 lb 5 oz. Winter rings end at about 4½, 9½, 15¼, and 19½ in., and an additional 1½ in. of growth is shown since it returned to the estuary in its fifth year (ref. 50/51, 35·19).

Appendix I

Sources of Data

Information about the rivers, such as the names, lengths, and areas of their basins, has been taken from the State Lands and Surveys Department's 4 miles to 1 in. map. River lengths were measured with a map-measurer as accurately as possible. This method used on a small-scale map considerably underestimates the actual length of the rivers, because their courses cannot be shown in detail at this scale. The figures given for river lengths, areas of basins, altitudes of head-waters, and mean gradients are only approximate. These, together with other relevant data, are summarized in Table 17.

Water flow figures, where given, have been supplied by the Hydro-Electric Commission of Tasmania. pH readings were made in the field with a Lovibond comparator. Temperature and pH measurements were made between 0930 and 1800 hr from April 17 to 22, 1950.

TABLE 17

COMPARATIVE DATA ON SOME RIVERS OF THE NORTH-WEST REGION OF TASMANIA

River	Length (miles)	Area of Basin (sq. miles)	Altitude of Headwaters (ft)	Mean Gradient (ft/mile)	Average Rainfall at Headwaters (in./yr)	Monthly Average Flow (cusecs)			Water Flow Measured at:		Temperature (°C)	pH
						Max.	Min.	Mean	From Coast (miles)	Altitude (ft)		
Duck	25	160	1000	40	40–50	—	—	—	—	—	13·0	7·1
Black	30	140	1000	33	60–70	—	—	—	—	—	—	—
Inglis	30	200	1500	50	50–70	—	—	—	—	—	11·5	7·1–7·2
Cam	25	100	1500	60	60–70	—	—	—	—	—	11·0	7·0
Emu	30	100	2500	83	70–80	808	4	150	16	1500	9·0	7·2
Blythe	35	135	2500	71	70–80	—	—	—	—	—	10·5	7·0
Leven	55	300	3000	55	70–90	4100	50	600	12	300	11·5	7·4
(at Loongana)	—	—	—	—	—	—	—	—	—	—	10·0	7·1
Forth	55	480	4500	82	60–90	6990	73	1200	7	260	11·5–12·5	7·0–7·2
Wilmot*	—	—	—	—	—	1278	6	300	28	1500	11·5	7·1
Mersey	100	700	3500	35	70–80	6020	27	1100	50	900	11·5	7·2

*The Wilmot River joins the Forth River above the point at which the Forth flow was measured.

THE SEA GARFISH, *REPORHAMPHUS MELANOCHIR* (CUVIER & VALENCIENNES) (HEMIRAMPHIDAE), IN SOUTH AUSTRALIA: BREEDING, AGE DETERMINATION, AND GROWTH RATE

By J. K. Ling*

[*Manuscript received September* 20, 1957]

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Summary

There are seven macroscopic gonad stages recognizable in male sea garfish, and eight in females with which ova diameter measurements have been correlated. In South Australia the spawning period lasts from late September to early March, and activity is most intense during October and November. A second period of breeding activity may occur in February. A few females are sexually mature at 2 years, but the majority do not spawn for the first time until the end of 3 years.

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This applies also to males. A latent maturation cycle is demonstrated in immature female garfish.

The use of otoliths for age determination is described and the method validated by Petersen length frequency polygons. The rate of growth has been deduced from calculated intermediate lengths of younger garfish, based on an otolith length/fish length relation and the mean lengths of older age groups. The weight of the garfish varies as the cube of the length. Females attain a larger average size than males after the third year. Gulf St. Vincent females grow faster than those in other regions; males, however, are variable.

Application of these results to a management policy for the commercial fishery is severely restricted by the inadequate official catch statistics. However, it is recommended that netting of garfish in Coffin's Bay be prohibited, but that no change in the minimum legal length should be made for the present.

I. Introduction

Among the inshore species of fish caught along the South Australian coast the sea garfish, *Reporhamphus melanochir* (Cuvier & Valenciennes) (Hemiramphidae), constitutes a substantial proportion of the annual catch. This amounts to between half and three-quarters of the total Australian sea garfish production, the remainder of which is caught largely in Victoria. Management of the fishery can only be carried out on the basis of biological knowledge of the species concerned, and this paper is presented in the hope that it provides data useful for wise utilization of the garfish in South Australian waters. Only breeding and growth aspects have been studied, but these are of sufficient importance to be published as a separate report upon which management regulations may perhaps be based.

The minimum legal length for sea garfish in South Australia is 8 in. from the tip of the upper jaw to the tip of the upper half of the tail. However, so little is known about the commercial fisheries in this State that the effectiveness of the present legal length is open to question. Moreover, inadequate catch records and routine market observations place a great load on the investigator, who must therefore collect all his own statistical data. The only catch records for South Australian sea garfish are of weights handled in the Adelaide market during the periods 1936–37 to 1945–46; these are taken from Annual Reports of the South Australian Fisheries and Game Department. In addition there are figures for total production for the years 1951–52 to 1955–56 (Kearns 1953–1955; Anon. 1956–1957). Figure 1 shows the annual amounts of garfish which came into the Adelaide fish market during 1936–37 to 1945–46. Legislation requiring the above data to be supplied by the markets came into force in September 1938, so that returns for the year 1938–1939 and subsequently should give fair indications of the trends. In the years following 1937–38 there is an obvious falling off in the amount of fish handled for which the 1939–1945 war can very likely be held responsible, although actual fishery effort cannot be gauged. After the war the total weights of garfish taken in the whole of South Australia were:

1951–52	500,000 lb
1952–53	750,000 lb
1953–54	650,000 lb
1954–55	386,650 lb
1955–56	402,000 lb

Again, without a knowledge of the effort expended in catching these fish no accurate judgment can be made as to whether or not overfishing has been practised, but a downward trend from 1952–53 onwards is becoming manifest, with only a slight improvement in 1955–56.

The almost total absence of data pertaining to small and undersized (below 8 in. total length) garfish is the most serious deficiency in the present study. However, the commercial catch has been well covered; fish from the smallest to the largest occurring in the markets have been collected and examined. Work commenced in April 1954 and concluded in December 1955. During that time the lengths of

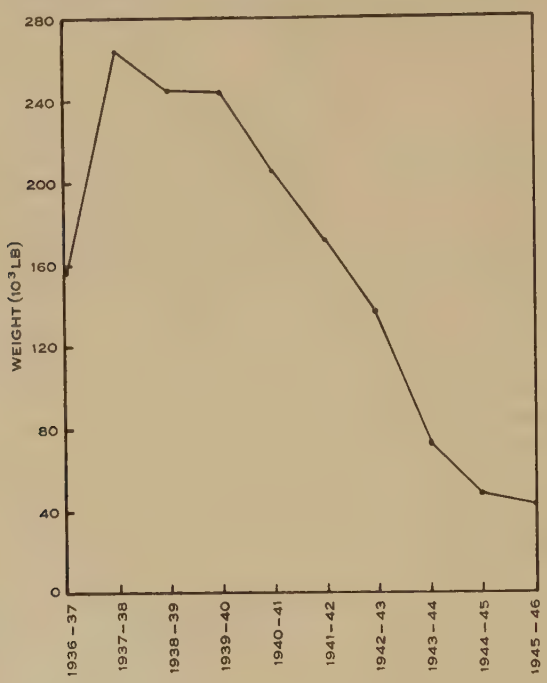

Fig. 1.—Amounts of sea garfish handled in the Adelaide market for the 10-year period 1936–37 to 1945–46.

15,739 garfish were measured and 2234 otoliths were taken for age and growth rate calculations. In addition, the macroscopic condition of many ovaries and testes was noted throughout the investigation, and microscopic examination of 570 ovaries was carried out for the same period.

II. Sources of Material

(a) *The Commercial Fishery*

Only the one species of sea garfish, namely, *R. melanochir*, is recognized as an important part of the inshore fisheries in South Australia. The annual weight landed has amounted to a quantity between half and three-quarters of a million pounds

(whole weight), which is exceeded only by the spotted whiting, *Sillaginodes punctata* (Cuvier & Valenciennes) (Sillaginidae), and the Australian "salmon", *Arripis trutta* Bloch & Schneider (Arripidae), among the inshore species.

Fig. 2.—South Australia, showing localities mentioned in the text or from which sea garfish material was obtained, and the three major subdivisions into which localities were classified: *A*, Port Lincoln region; *B*, Spencer Gulf region; *C*, Gulf St. Vincent region.

21.	Adelaide	10.	Moonta	12.	Port Victoria
2.	Baird Bay	15.	Penneshaw	17.	Port Vincent
1.	Ceduna	18.	Pine Point	20.	Port Wakefield
3.	Coffin's Bay	6.	Point Lowly	22.	Robe
14.	Corney Point	8.	Port Broughton	16.	Stansbury
5.	Cowell	4.	Port Lincoln	11.	Tickera
13.	Hardwicke Bay	7.	Port Pirie	9.	Wallaroo
19.	Melton				

Although fishermen report the occurrence of deep-sea garfish up to 100 miles offshore, the commercial fishery is essentially an inshore one. The garfish are caught in hauling (beach seine) nets operated over shallow flats where the fish come together to feed on "sea-grass" (*Zostera* sp.). Extensive flats of this plant occur in Spencer

Gulf and Gulf St. Vincent, as well as in American River on Kangaroo Island. There are similar situations at the eastern border of the Great Australian Bight at least as far west as Ceduna. Localities from which garfish have been taken for the purpose of this study are shown in Figure 2, which also shows the three regions referred to below. Only the south-eastern portion of the State was not represented; here a limited fishery exists near Robe, but the small amount of garfish goes straight to the Victorian markets and none reaches Adelaide. The rest of the species range has been covered by material collected or examined in fish-processing works at Adelaide, Port Lincoln, and Ceduna. On account of this, only fish above the minimum legal

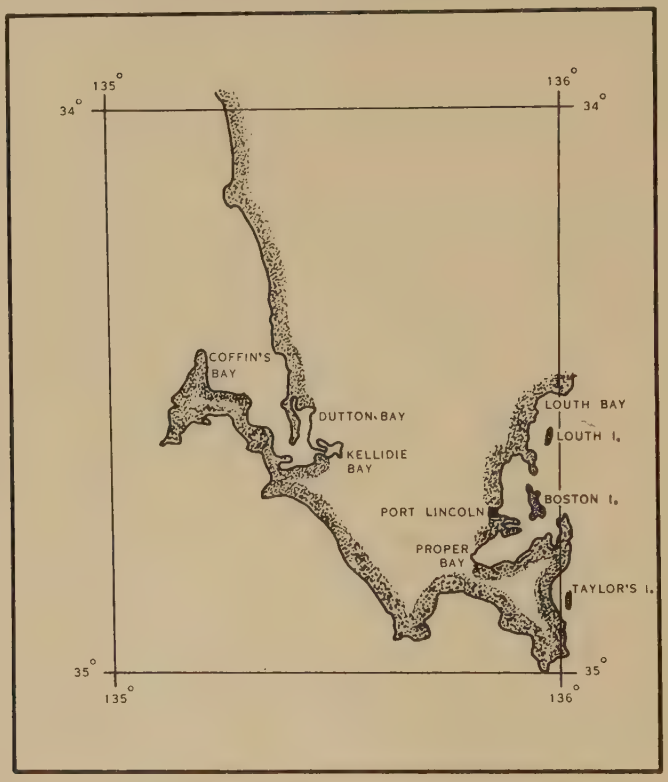

Fig. 3.—Localities in the Port Lincoln region.

length have been studied, with the exception of a few under-size fish sometimes seen in the markets and a special sample caught with a fine-meshed net constructed for the purpose of obtaining small garfish.

The material has been allocated to one of three regions depending on the point of capture, which can be ascertained with certainty from processing works managers. These regions have been arbitrarily determined without regard to physical or biological properties. Port Lincoln and its immediate environs constituted an area of more intense study, while Spencer Gulf and Gulf St. Vincent are two natural divisions. The localities within the Port Lincoln region from which garfish came are shown in Figure 3. The limits of the three regions are defined below:

A. The Port Lincoln region is roughly bounded by longitudes 135° and 136° E. and latitudes 34° and 35° S. It therefore includes the Coffin's Bay area.

B. The Spencer Gulf region is all that body of water lying north of latitude 35° S., and excluding parts of the Port Lincoln region as designated above.

C. The Gulf St. Vincent region comprises all that area of water and is bordered in the south by Kangaroo Island, longitude 138° E. being its western limit.

Material from each of these major areas was treated separately, for the sake of both convenience and comparison. Where variations become obvious in fish from localities far apart, these differences may be explicable on the basis of known physical properties of the regions. This South Australian investigation may be regarded as a model upon which further racial studies over the greater part of southern Australia can be based, and with which wider comparisons will be possible.

(*b*) *Efficiency of the Sampling Technique*

Buchanan-Wollaston (1927) discussed the selective action of nets and its possible effect on the sampling of fish populations. Kesteven (1950) also dealt with this question, which is relevant to the present study since garfish are captured commercially by means of hauling nets. Kesteven's conclusion was that where nets are repeatedly employed in a commercial fishery, or in sampling, the selectivity is reduced or almost negated. The very occasional occurrence of even under-size garfish among the market batches bears out this assertion. Moreover, the fishermen themselves must often sort the catch in order to release the very small garfish which are captured along with the commercially valuable ones. Hence it is probable that the garfish examined in the markets did represent the true population at least in so far as fish above a length of 8 in. were concerned. This is assumed for the purpose of the present study.

Fairbridge (1951) was confronted by the problem of net selection in his investigation of the New South Wales tiger flathead, *Neoplatycephalus macrodon* (Ogilby) (Platycephalidae). The size range observed in market samples was found to differ from that of collections made by means of an experimental trawl the cod-end of which was covered by a fine-meshed net. One sample of garfish was taken in Coffin's Bay using a lamp and a fine-meshed dip net on the night of May 14, 1955. There were only 94 fish altogether and, since no commercial catch was taken from the same area at or about that time, it is not possible to compare the sample very closely with the size ranges met in the markets. The best comparison is that between the experimental fish and commercial hauls made about 1 month before and 1 month after May 14 within Coffin's Bay. In Figure 4 the length frequency curves of the three hauls are plotted, the frequencies being expressed as percentages of the total number of fish in order to eliminate differences due to variation in sample size. It is obvious that fish between the lengths of 17 and 24 cm are more abundant in the experimental catch than in either of the market samples. This includes fish above the minimum legal length of 8 in. (20 cm total length, or 18 cm length to caudal fork) which would very likely be retained by the fishermen if and when sorting became necessary. Without more data it cannot be stated at what size

net selection ceases to be operative; but its effect seems clearly manifest in a somewhat false representation by market samples of the real nature of the garfish population as regards overall size range. Such sampling discrepancies must be borne in mind, and anomalous biological results may be explained by the selectivity of the material. The experimental haul is deemed to represent the natural population more closely than samples examined in markets and other places where only commercial catches were available for study. In the latter, however, fish over 8 in. in total length are held to represent the size composition in the older groups.

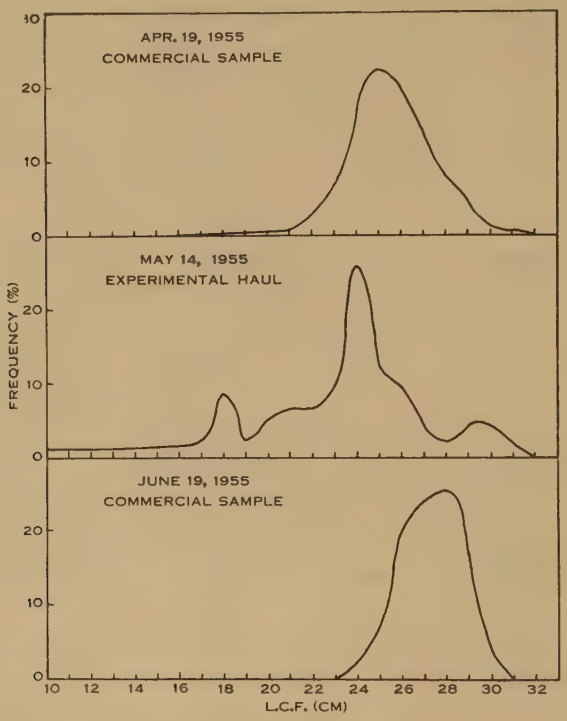

Fig. 4.—Comparison of length frequencies of an experimental haul (*centre*), using $\frac{1}{2}$-in. mesh, and of two commercial catches using $1\frac{1}{8}$-in. mesh, all from Coffin's Bay.

III. The Spawning Cycle

(*a*) *General Remarks and Methods*

Briefly, the methods by which the breeding activity of a fish may be studied include a survey of the seasonal variation in the condition of the gonads through the year. This involves a study of the macroscopic appearance of the gonads and a histological examination including ovum diameter measurements. Since it may be assumed that the seasonal rhythm is adjusted in the two sexes so that the spawning acts coincide, knowledge of the seasonal gonad cycle of one sex will be enough to determine the general picture. In previous fishery investigations (e.g. Clark 1934; Hickling and Rutenberg 1936; Fairbridge 1951) the female cycle has

come under review, since its study is probably simpler and, moreover, it is the fate of the egg with which the fishery biologist is ultimately concerned. Detailed histological work has shown that in some species the maturation rate of the gonads differs in the two sexes (Burger 1939; T. D. Scott 1954). The present survey is aimed at deriving only the time of spawning; the histology of the gonads has not been touched upon.

During the collection of gonad material the macroscopic condition of the gonads in both sexes was noted. Every month up to 50 ovaries and 10 testes were obtained from garfish caught in various parts of South Australia and brought in to the Adelaide and Port Lincoln markets. Only the ovaries were subjected to further examination. The data recorded for each fish from which a gonad sample was taken included:

(1) Length from tip of upper jaw to the caudal fork (L.C.F.).

(2) Length from tip of upper jaw to tip of tail in its normal position—"natural" total length (T.L.).

(3) Weight in grams (recorded only subsequent to May 1955).

(4) Sex.

(5) Macroscopic condition of gonads.

Both otoliths were also collected from the sacculus and stored in envelopes numbered to correspond to the data sheets but with no other information thereon. Ovaries were preserved in 5 per cent. formalin.

It was the object of this aspect of the investigation to study the seasonal changes in the gonads of a complete size range of the garfish population. Some selection was necessary to ensure that all sizes were sampled in any one month. No details were known concerning the gonad condition until the fish were selected; hence the study of the breeding cycle was quite objective. Length frequencies were recorded from at least 200 fish, of which the gonad sample was part, in order to gain an idea of the size composition. The sex ratio within the 200 or more fish was determined by sexing every individual.

The study of the breeding cycle in the garfish resolved itself into a month by month comparison of the macroscopic condition of the gonads of males and females and a microscopic examination of ovaries, including ovum diameter measurements. The rest of this section deals with the seasonal changes which were observed in the condition and size of gonads and ova respectively.

(b) *Macroscopic Condition of the Gonads*

(i) *Classification of Gonad Stages*

When gonad samples were being collected attention was paid to the macroscopic appearance of the sex organs and surrounding viscera. In this way it was hoped to discover the changes consequent upon spawning and, if possible, to relate these external features to the more detailed microscopic studies carried out at a later date.

Hjort (1910) described seven different gonad conditions in both male and female herring of the eastern North Sea and Icelandic waters. Other workers have since followed Hjort's scheme of gonad stages. Some of the investigations dealt only with these macroscopic stages, while others have compared them with microscopic ovum diameter counts; and histological examinations have also been carried out (Hickling and Rutenberg 1936; Partlo 1955). Graham (1924) investigating the cod, Hickling (1930) the hake in Europe, and Fairbridge (1951) the New South Wales tiger flathead, all adopted Hjort's classification, with certain modifications to suit the particular species.

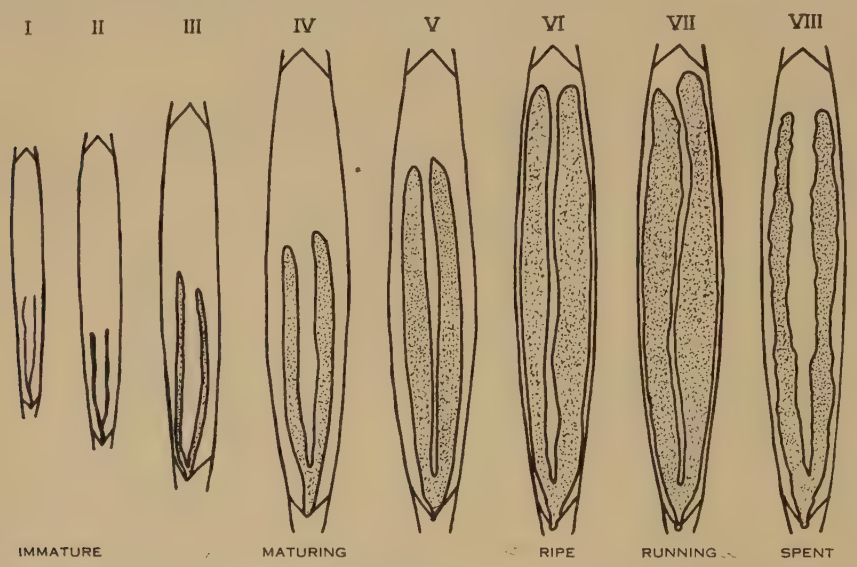

Fig. 5.—Size and shape of ovarian stages I–VIII in relation to the body cavity (about one-third natural size).

FEMALES

Hjort used seven stages in his classification of gonad conditions; but an eighth, a very immature state of the ovaries when the sex is indistinguishable, is recognizable in the garfish. These eight stages have been arrived at on their macroscopic appearance only and may or may not be functionally distinct. Their significance can only be assessed by microscopic examination, but they should be comparable with the herring categories since mature ova of this fish are also large, but still only about 1·5 mm in diameter or less than half the size of ripe garfish eggs. In Figure 5 the eight ovarian stages are shown in relation to size of the body cavity.

Stage I.—Immature virgins. Ovaries small and thread-like, extending about one-third of the length of the body cavity. Sometimes only just visible; and it is almost always impossible to distinguish the sex. No ova visible.

Stage II.—Immature virgins. Ovaries distinguishable as such. Small and thin, about $\frac{1}{16}$ inch in diameter, occupying same space as stage I and in the body cavity. White in colour or translucent; individual ova not visible.

Stage III.—Maturing virgins or recovering or resting mature (spent) fish. Ovaries about $\frac{1}{8}$ inch in diameter, extending half way along length of body cavity. A blood-vessel runs along dorsolateral surface of gonads, with smaller ones ramifying over the more posterior region. Small white ova to be seen in translucent ovaries.

Stage IV.—Maturation continuing. Ovaries about same relative length as in stage III but twice as thick. Blood-vessels larger. Ova plainly visible, having a diameter of about 1 mm.

Stage V.—Maturation still in progress. Ovaries about $\frac{1}{3}$ inch in diameter, extending some three-quarters of the way along length of body cavity. Blood-vessels ramifying over the ovaries are reduced, but the main dorsolateral ones still large. The ova appear to be clearing and are about 1·5 mm in diameter.

Stage VI.—Ripe ova, but not yet running. Ovaries lie along the entire length of the body cavity and have become much swollen to about $\frac{3}{4}$ inch diameter. Only the large lateral blood-vessels obvious. Ripe ova 3 mm in diameter appear as a clear, yellow-green, jelly-like mass and are quite firmly packed, the ovary being fairly turgid. There is no sign of the genital pore being open. Smaller ova constitute a second group; diameter about 1·5 mm.

Stage VII.—"Running ripe." Ova shed through genital pore when slight pressure is applied to the abdomen. If some ova have been extruded the ovaries will be somewhat limp and flaccid, with the remaining large ripe ova lying free in the lumen. Blood-vessels running along the side of each ovary are still very big and clearly defined.

Stage VIII.—Spent ovary. May or may not be bloodshot, but very limp and shrunken. Tunica tough and leathery, unlike easily ruptured ovarian wall of ripe stage. Blood begins to appear at the posterior end where the ramifying vessels were obvious in the earlier stages. Only a few residual large ova remain, but many "medium-sized" ones of the next smallest group still visible.

MALES

Macroscopic gonad conditions in the males were confusing and it was not possible to recognize a great many distinct stages. Hjort classified the herring males according to seven stages as in females. Seven are also distinguishable in garfish, i.e. one less than the number of female gonad stages. Figure 6 shows the relative sizes, shapes, and spaces occupied in the body cavity by tests in the various categories, which are classified as follows.

Stage I.—Immature virgins. As in stage I of the females: sex indistinguishable; the gonad a mere thread-like structure, about one-third the length of the gut space.

Stage II.—Immature virgins. Sex just recognizable. Testis a little thicker than in stage I, and of noticeable "brittle" structure as distinct from the somewhat elastic ovary; still extending about a third of the way from the anal end of gut cavity; coloured yellowish cream.

Stage III.—Maturing virgins or recovering or resting spent adults. Cream in colour and displaying a triangular cross section about $\frac{1}{10}$ inch across. Same relative length as earlier stages.

Stage IV.—Maturing (though easily confused with spent). Colour brownish pink. About $\frac{1}{8}$ inch in cross section, extending half way along the body cavity. Posterior end more tubular and white.

Stage V.—Mature, but milt not yet running. Pale pink in colour, and swollen to about $\frac{1}{4}$ inch across, extending half way along the body cavity. Triangular shape still obvious. Tubules visible as a tightly coiled mass. Pink colour gives way to white at posterior end, where milt is accumulating. A median blood-vessel visible in hinder region and giving off branches to each testis.

Stage VI.—Running ripe. Testes even more swollen. Very soft, and pale pink in colour with black spots on surface. Strap-like in general shape, with tubules plainly visible in the body of the organs. Genital pore open and white milt exuded by the application of slight pressure on the abdomen.

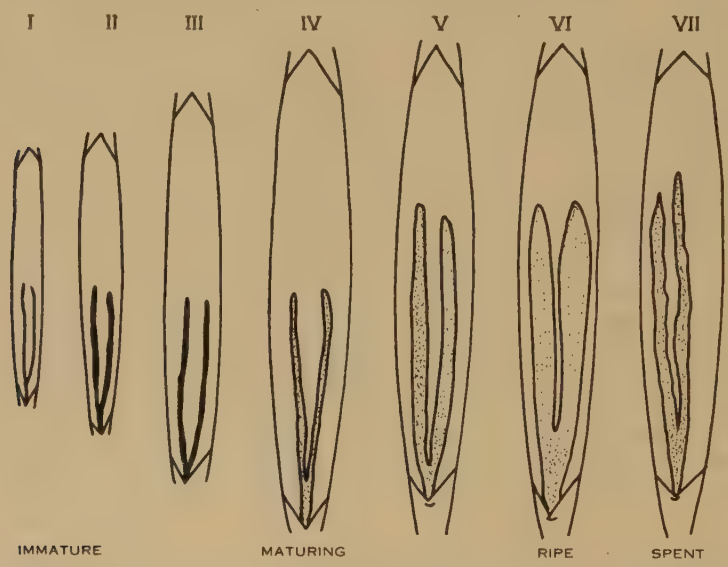

Fig. 6.—Size and shape of testis stages I–VII in relation to the body cavity (about one-third natural size).

Stage VII.—Spent. Much reduced in size and showing signs of blood, which colours the testis a dull reddish brown.

(ii) *Seasonal Changes in Gonad Condition.*—By noting the condition of the gonads over a period of a year it should be possible to gain a fairly clear insight into the spawning cycle of the fish. This applies especially to the larger mature fish which have certainly spawned before; in juveniles destined not to spawn in the current year, and fish maturing prior to their first spawning activity, the course of events is a little more complex. The results of the macroscopic observations could be expressed quantitatively by stating the number of fish in any one stage at a particular time, but this method is rather subjective, so that the breeding cycle must be studied by observing variations in condition of the gonads in the course of a year.

During April and May 1954 gonads were, without exception, classified only as belonging to stages I, II, or III. No further observations were made until late September, when great changes had occurred. Many fish were in "ripe" condition (stage VI), while all others showed gonads in stages IV and V, except one small fish which still had stage II ovaries and presumably would not be participating in the spawning activities during the forthcoming season. Ova were running freely from many fish in the months October, November, and December; the incidence of running ripe females was less in December than in the previous two months.

Spent ovaries became noticeable in January, but running ripe females were still encountered. This condition continued through to March, with increasing numbers of spent females and no evidence of spawning after the first week in March.

During the next 4 months the gonads were typical of recovering spent fish or maturing virgins. In the females the last signs of blood-filled ovaries persisted until as late as mid July 1955, but this was an isolated case and by the end of June the majority of the ovaries were in stage II, III, or IV condition. In August development of the gonads became obvious; although no ovaries had advanced beyond stage IV most of them had attained this condition. This was observed at the end of August and persisted until mid September, when a few ovaries were noted to be at stage V, while one had reached stage VI. Thus the maturation period is of short duration between June or July and September, when spawning begins again.

Observations on gonads in September 1954 were carried out on Port Lincoln garfish, while those for the same time in 1955 were concentrated on fish from the northern part of Gulf St. Vincent. Examination of the Port Lincoln fish took place on September 23, 1954, and of the Gulf St. Vincent specimens on September 19, 1955. Within the limits of the method of study, the females of both regions could be described as showing identical gonad conditions. It seems that spawning in the two areas (separated by about 200 sea miles) commences almost simultaneously.

As stages VI and VII were approached, feeding activity appeared to stop. In all cases empty guts were the rule when ovaries were almost ripe. The entire body cavity then became occupied by the greatly swollen ovaries. However, the mesentery of the gut was often taken up with fat tissue early in the spawning season. This fat became reduced as time went on, and after spawning had been completed in any one fish, it was rare to find any still present in the body cavity.

(*c*) *Microscopic Study of Ovarian Material*

(i) *Methods.*—A quick but informative method of assessing the seasonal variation in the ovaries is that of Orcutt (1950) who established the spawning period of the starry flounder, *Platichthys stellatus* (Pallas), by making measurements of the largest ova in a representative sample from each of a number of ovaries. The mean maximum ovum diameter for each ovary is determined and the frequency with which a particular size occurred is recorded on a chart, as shown in Section III(*c*)(iii). This method results in a more objective estimate of the time and duration of the spawning period. Ovarian material has been collected and examined over a period from April 1954 to December 1955, with gaps in the record for June, July, and August 1954, and October and November 1955.

Depending on the availability of suitable (i.e. fresh) fish, ovary samples were collected from as many as 56 garfish in one month down to only 11 during another. Generally, 30–40 ovaries were collected each month, and the total amounted to 571 for the whole survey. From the central region of the left ovary a piece about 1 in. long was taken, cut into two portions, and preserved in formalin. Where the left ovary was damaged, as was so on a very few occasions, the right ovary was sampled instead. These pieces of ovary were broken up and teased out in water on a microscope slide until all the ova were thoroughly separated. The ovum diameters were measured by means of a low power binocular microscope fitted with a micrometer eyepiece. Ten or a dozen of the very largest ova sufficed to give a mean maximum reading.

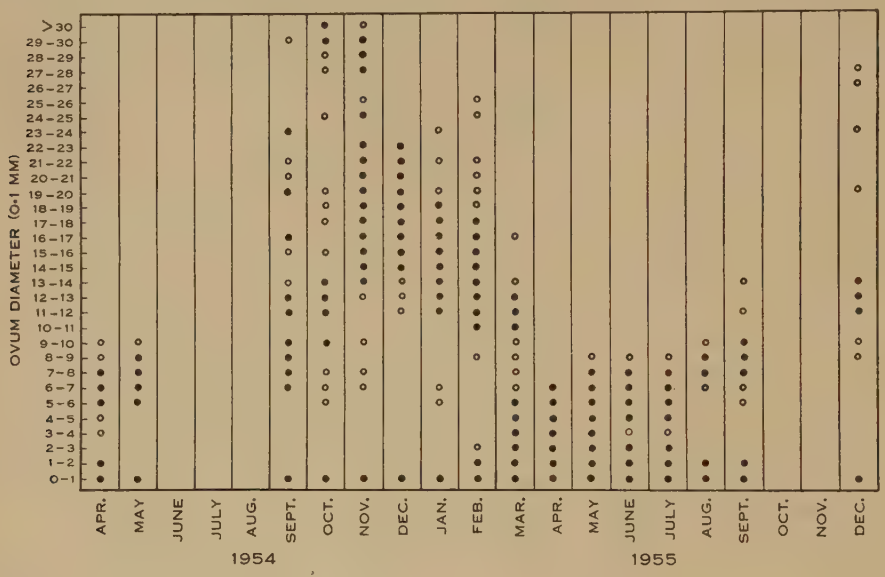

Fig. 7.—Monthly size progression of ova of mature (III group and over) sea garfish, 1954–1955. The columns of circles show the total range of maximum diameters. Solid circles show size ranges of the largest ova of the majority of females. The fact that columns of solid circles are separated by open circles implies that substantial numbers of fish had varying mean maximum diameters, which suggests that ripening was not contemporaneous amongst all fish.

The ovum diameter frequencies were also determined for a number of additional ovaries each month. Two to three hundred ovum diameters were measured on eggs of all sizes in each ovary. Clark (1934) regards this number as giving adequate representation in mature ovaries, while somewhat fewer (at least 100) ovum diameters are enough for the immature groups. All eggs were measured along the diameter lying parallel to the horizontal cross-hair of the micrometer eyepiece. Badly distorted ova were neglected; otherwise all were measured, some along short axes, others along the longer axis (in the case of oval eggs); and across a random diameter of the round ova. This has been shown to provide a reliable estimate of the ovum diameter frequencies (Clark 1925). It was found that no significant variation existed

between the size frequencies of eggs from anterior, mid, and posterior regions of the ovary; but the central part was always taken for convenience.

(ii) *Monthly Progression of Ovum Diameters.*—Owing to the large size of ripe ova, they are well separated from the next group of maturing eggs. In actual fact four distinct ovarian groups were encountered in ripe ovaries. A similar finding was recorded for *Cypsilurus oligolepis* (Bleeker), an exocoetid fish which also possesses very large ova when ripe (Prabhu 1956). Consistent with those of earlier workers, notably Hickling (1930) and Raitt (1932), a scheme of classification is possible for the four groups of garfish ova. Prabhu also used this older grouping, which is applied to the garfish ova as follows:

(1) Immature ova.—Very small, angular ova; transparent and with nucleus clearly visible. These tiny ova measured up to 0·2 mm in diameter.

(2) Maturing ova.—Smallest opaque ova, diameter from 0·2 mm upwards. The smallest of this group are just beginning to accumulate yolk granules, while the larger ova are quite opaque, so that the nucleus cannot be seen. The size ranges from about 0·2 to 1·0 mm.

(3) Mature ova.—Large opaque ova, pale yellowish in colour and having a diameter up to 1·6 mm. The sizes are usually distinct, but the smaller ova may merge with group (2). These ova have still not been released into the lumen by rupture of the follicle.

(4) Ripe ova.—Large, transparent ova up to 3·5 mm but as little as 2·5 mm in diameter. Covered by adhesive filaments equal in length to the egg diameter. These ova lie free within the lumen and are easily stripped from a gravid female with a little pressure on the abdomen.

The largest average ovum diameters are most abundant during October and November, and to a lesser extent in September and December (Fig. 7). Spawning is thus at its greatest intensity during early summer, and late spawners carry on until February. A sharp drop in the overall size of ova marks the spent and recovering stages, which are followed by a period of quiescence during May, June, and July. Maturation begins late in July and proceeds through to September, at the end of which month early spawners become active.

Throughout the year there is a residue (Hickling's (1930) "reserve fund") of tiny ova. These are angular and quite transparent, so that the nuclei are visible. In June an increase in size of a group of ova from this reserve fund becomes obvious and, as maturation continues, the larger ova continue to grow until ripeness is attained. It is obvious that the final phase of maturation between August and September is marked by a sudden enlargement of the ripening ova.

The large size of the ripe garfish ovum is a noteworthy feature. Orcutt's (1950) method is particularly suited to analysis of these large ova, since the numerical strength of the various groups of ova is not allowed to mask the general picture. The drawback to the method is that no idea is given of the other ovarian groups present in a single ovary at any one time of the year. When it is considered that one ripe ovum (diameter about 3 mm) occupies a volume of approximately 14 cu. mm, the significance of a few such eggs becomes lost when they are compared

numerically with the next group of ova (diameter about 1 mm), which have not reached the ripe stage. Orcutt's method and the ovum diameter frequency method must, however, be complementary to one another.

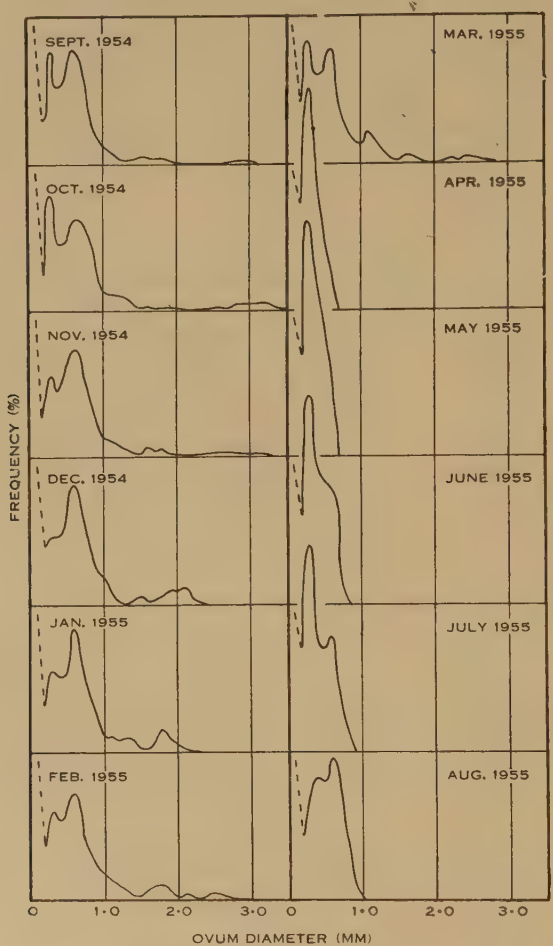

Fig. 8.—Ovum diameter frequencies for mature garfish (age groups III and over) for the 12-month period September 1954 to August 1955.

In order to study the annual cycle in mature fish initially, percentage frequency diagrams have been drawn up for ovum diameter measurements in fish 3 or more years old, commencing in September 1954 and going through to August 1955 (see Fig. 8). The small restin ova ar still not represented in their true proportions, but groups of maturing ova distinguish themselves. During the spawning season, September to November, the large, ripe ova stand out greatly larger than the next group of maturing eggs. The latter are depicted as having a mode around the 1–1·5 mm size, which can be seen progressing (with enlargement of the ova) during

January and February, when a few spawning fish still persist. It would appear from a study of the ovum diameter frequency polygons that there is a second spawning phase during January and February. A general decrease in the size of ripe ova is obvious towards the latter part of the breeding season. The rather big range in the diameters of these ova was noticeable; clear, filamentous ova (i.e. recently released from the follicle) measured from about 2·5 to 3·5 mm across. In March a few large ova remain but the majority are of the order of 1·5 mm or less in diameter. By April there is no sign of any but very small immature ova. March probably represents the time of most spent ovaries. During April, May, and June the small reserve fund eggs are represented by a single mode in the graph, although there is a second peak beginning to form in June which becomes more obvious in July and August as a group of ova starts to mature.

Clark (1934) found that the multiple modes occurring in ovum diameter frequency polygons for the California sardine were suggestive of more than one spawning act per season by a particular fish. Prabhu (1956) drew a similar conclusion for *Cypsilurus oligolepis* from the presence of a wide size range of mature ova. The same holds true in the garfish, but it should be realized that the polygons are derived from composite sets of data for any one month and individual fish habits will be masked. It was noticed in handling ripe females, however, that some contained tightly packed ovaries while others had ovaries still with many ripe ova present but much less turgid. This at once suggested that all ripe eggs may not be released simultaneously.

The fate of the third (maturing) group of ova appears to be resorption at the end of the season. The mature ova enlarge, ripen, and are shed in March at the very latest; then there is a sudden return to the resting or recovery stage. In fact a great deal of resorption is proceeding during March. It is likely, however, that the sea garfish either spawns at least twice, or the ova are released gradually as they ripen. The spawning period, which is rather protracted, lasts from late September in the case of the earliest participants to early March for the late breeders.

(iii) *Gonad Stages and Ovum Diameter Frequencies.*—Ten examples of each of the ovarian stages II–VIII were selected and ovum diameter frequency polygons were constructed for them. Full representation of the quantitative ovum groupings was still not possible, because of the enormous numbers of tiny ova. These form a distinct modal group at all times of the year, although they are not so obvious during the spawning season (see Fig. 9). In stage II the whole stock of ova consists of this immature group. Stage III shows an increase in size to be taking place, without the appearance as yet of the distinct second group of ova which becomes obvious in stage IV and persists throughout this and the four succeeding stages. The mature group (3) ova are present in stage V onwards, but are not depicted as modes. Finally, in stage VI, the sudden onset of ripening has caused the group (4) ova to become quite separated from the remainder of the stock. The presence of an unbroken series of large ova from group (3) to group (4) in stage VII suggests that, in a running ripe female, mature ova are all the time moving into the ripe batch. Spent ovaries (stage VIII) contain small immature and maturing ova, along with a

residue of mature ova which are resorbed or otherwise disappear from the resting ovaries.

It is clear, therefore, that the recognizable gonad stages observed by macroscopic examination of ovaries do bear a relation to microscopic changes which proceed throughout the annual cycle. It is also obvious that the ovum diameter frequency polygons for stage IV (maturing) and stage VIII (spent) ovaries are very similar. In fact, without the appearance of blood flecks in the ovary, it was not always easy to classify the gonads as maturing or spent. Bowers (1954) was

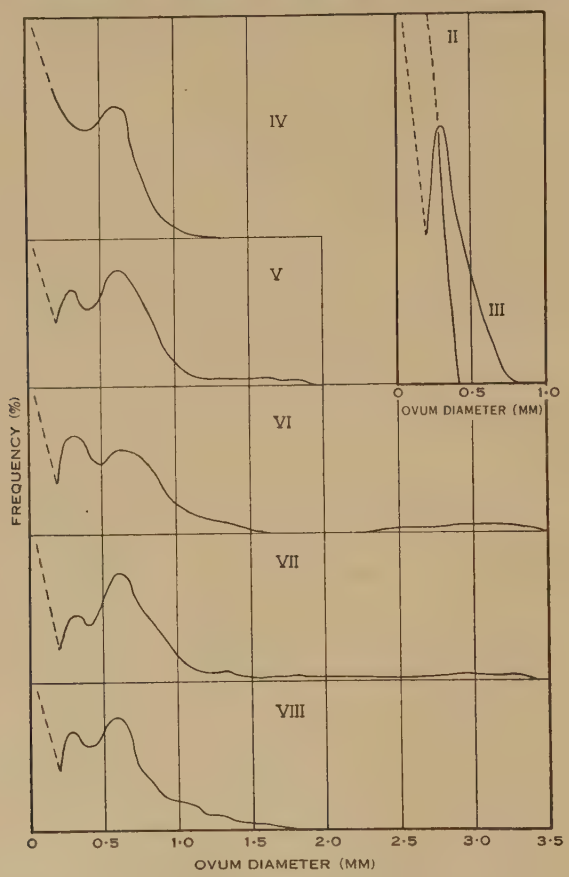

Fig. 9.—Ovum diameter frequencies for seven ovarian stages, II–VIII. Stages II and III are combined in the one figure.

able to distinguish between these stages in the European whiting by the presence of yellow bodies to which he ascribed the term corpora lutea. Yellow bodies were found to be abundant in garfish ovaries towards the end of the spawning season; they first became obvious late in December. Jelly-like masses were also seen in spent ovaries of the White Sea wolf-fish, *Anarhichas lupus* Linnaeus, by Barsukov (1953) and these may be analogous to Bowers's corpora lutea. That corpora lutea–

like bodies of fish are in fact functional has been suggested (Bullough 1951). However, the proof for the existence of these glands in the garfish must be based on more extensive study than has been carried out in the present investigation.

(iv) *Ovarian Cycle in Virgin Females.*—It was found while studying seasonal changes in the macroscopic condition of ovaries that during the resting part of the annual ovarian cycle the sex even of mature garfish was often obscure. Their ovaries may revert almost to stage I or II, with no visible ova. Later on towards the breeding season, however, sexual dimorphism became marked and ovaries of even very small garfish were distinguished as such. In other words there did appear to be a foreshadowing of the reproductive cycle in the mature garfish by a juvenile cycle or "pseudo-maturation". Hickling (1935) has already demonstrated that the young hake ovary passes through a series of seasonal changes which parallel very closely the mature sexual cycle. These changes seem to be under the control of an inherent factor which is itself to some extent regulated by the outside environment (Bullough 1939, 1940).

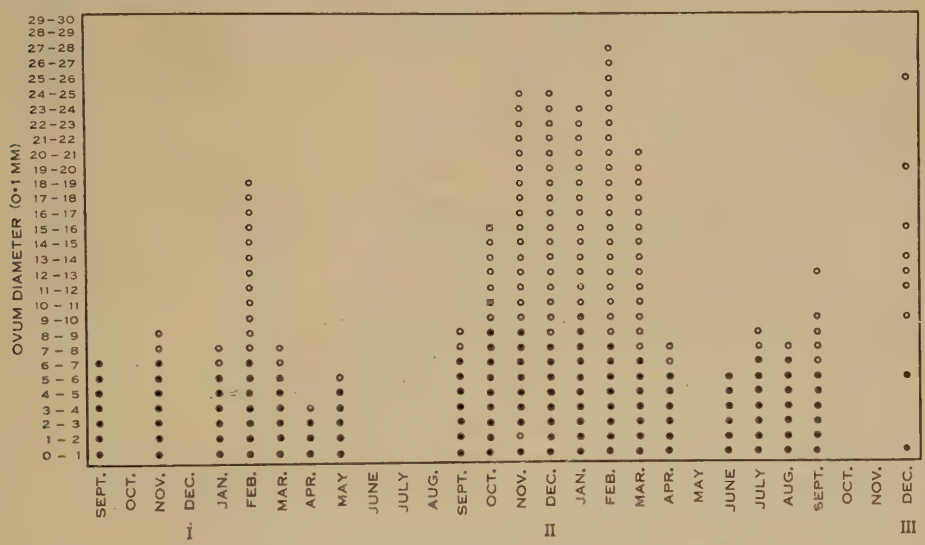

Fig. 10.—Monthly progression of ova of immature (I–III) garfish, 1954–55. Solid and open circles are applicable as in Fig. 7.

Orcutt's (1950) method is again used to demonstrate the c urse of events in the juvenile ovary and up to the time of first maturity. In Figure 10 the seasonal progression of ovum diameters is graphed for the immature garfish; i.e. they apply to fish of ages from about 9 months to 3 years (actual age). Since the collection lasted for only 16 months some doubling up has been necessary: fish of age groups II and III for the year 1955 have been used, in order to portray a continuous series for fish from 1 to 3 years old. This presupposes that the stages in the spawning cycle are the same from year to year. No variations were apparent between the mature cycles of 1954 and 1955; so that the immature fish also are assumed to follow the same pattern each year. Since the means of telling the age of fish must

be known if the year by year ovarian cycle in the young fish is to be followed, many of the points raised in Sections IV and V are assumed in this discussion. Fish separated on the basis of age by the otolith method did show different ovarian conditions.

Beginning in September 1954 with fish almost 1 year old (i.e. age group II), minute ova are dominant. The sudden increase in average maximum ovum diameter in February is inexplicable, but there is a remarkable parallel to the secondary progression of large ova seen in the mature ovaries. By this time nearly all the fish should be 1 year (plus a month or two) old. The presence only of smaller ova in March and April and a slight increase in size again in May closely follows the pattern in mature fish. In September, when the fish are approaching the age of 2 years, enlargement of some ova has taken place beyond that shown the previous year. Further increase in the size of the ova occurs up to 2·5 mm; and again in February the greater enlargement takes place. The sizes of the largest eggs do not equal those of ripe ova in the older garfish. However, some were obviously ripe with filaments visible. Small mean ovum diameters typify the March, April, and May ovaries, and maturation appears to commence again in June or July. The picture for September to December when the fish are nearly 3 years old is incomplete, but maximum ovum diameters show a steady increase. This tends to correspond to the pattern of ripening ovaries in mature adults.

It is clear that a cycle of incipient ovum maturation is displayed in the ovary of the immature garfish. In the month immediately preceding spawning (September), for example, there is a progressive increase in the maximum ovum diameters in age groups I, II, and III; but there is always a reversion back to much smaller ova groups during the following early winter (April, May, and June), i.e. larger ova are probably resorbed. On the whole, however, the monthly ovum sizes are all smaller in these immature fish than they are in adults for the corresponding month. Nevertheless, the seasonal development of the immature ovaries, as suspected from macroscopic observations, does seem to be real; and the existence of an internal rhythm corresponding to that reported for the immature hake is clearly demonstrated.

It is also clear that at least some female garfish spawn at the end of their second year of life. The number, however, is small; most spawners were from 2 to 3 years old and over. If virgin fish destined to spawn in the ensuing summer have ovaries developed only to the extent shown in September, the period when ripeness is attained will be later than in the older fish, which show a more advanced ovarian development in September. That the older fish do spawn earlier than the maturing virgins does seem probable on the face of this evidence.

(*d*) *Breeding Habits*

(i) *Spawning Behaviour.*—As previously described, the ripe garfish ovum is a large, clear, filamentous structure which probably becomes attached to weed at the bottom of shallow, sheltered bays such as those at the heads of the two gulfs in South Australia. Some attempts were made to secure a collection of eggs by working over the *Zostera* flats at the head of Gulf St. Vincent but without success. A single egg which could have been from a garfish was obtained at Encounter Bay on the south

coast on October 29, 1955, but this material was insufficient for any reliable conclusions to be drawn.

Graham (1939) reports having found eggs of the New Zealand garfish or piper, *Hemirhamphus ihi* (Phillips), attached by means of filaments to weed in tanks. Similar eggs were also discovered in weed found in the stomachs of mullet caught in the same haul as some garfish. Phillips (1921) observed that the New Zealand garfish spawns in early summer over its entire range, which covers nearly all of that country's coastline. Females 9 in. long, of weight 4 oz, contained ripe ovaries. It is known (Ling, unpublished data) that the New Zealand garfish is relatively smaller than its Australian counterpart; however, the spawning habits of the two species seem to resemble one another. By analogy, therefore, it seems likely that the eggs of *Reporhamphus melanochir* are shed and become attached to weed where development takes place. Vast shoals of tiny garfish are obtainable at these same localities a few months after spawning takes place.

There is an indication that the sexes segregate into spawning shoals. The evidence consisted of the preponderance of one sex over the other in many length frequency counts made during the spawning seasons of both 1954 and 1955; and is presented as follows:

Late October 1954.—Only 11 females among a sample of 309 garfish from Louth Bay. The gonads of the 298 males were mostly at an advanced stage of maturity.

Mid November 1954.—Four males and 190 females from Taylor's Island. The females consisted of ripe, running ripe, and spent individuals; so that this could be described as a spawning aggregation.

Mid December 1954.—Females again vastly outnumbered males in the fish examined during this period. The sample was made up of large fish, all with gonads in the ripe, spawning, or spent condition.

Mid December 1955.—Two samples from Wallaroo, but deemed to be of the same stock on the basis of length frequency studies, were made up of about 90 per cent. of females and 10 per cent. of males. Small fish were present with the larger ones, but the stages of ovarian maturity were very distinct; they were either quite immature or advanced, with many running ripe and spent ovaries present.

The overall sex ratio for 2844 fish examined between May and December 1955 was 63·4 per cent. of females to 36·6 per cent. of males. This lot covered the size range 17–37 cm L.C.F. Since the larger fish tend to be females the predominance of that sex in the market samples becomes very apparent. Had there been more small fish available it is possible that the sex ratio would have approached 1 : 1.

Spawning fish ceased to feed after about September. Feeding was resumed early in the following year, or after spawning had been completed in the case of late spawners.

Although it was not obvious in market observations that large fish matured earlier in the breeding season than small fish, a more detailed examination of the data indicates that there is a slight difference between the maturation rates of

large and small fish (Table 1). Larger fish appear to ripen at an earlier date than the small individuals probably just attaining their first maturity, which is in agreement with the conclusion reached in Section III(*c*)(iv). This more rapid development of gonads in older fish is not an unusual feature; a similar effect was observed in European whiting (Bowers 1954). The fairly small size range of garfish which would be mature (27–37 cm) could not be expected to reveal any but a very distinct variation between the size groups in which sexual maturity is first reached. The rate of development of the gonads may be a function of age, just as the attainment of sexual maturity should be if an internal rhythm controls gonad maturation. It was not possible to examine male garfish to determine the trend in rates of ripening of testes in the two size groups or in different age groups.

TABLE 1

MONTHLY GONAD MATURITY STAGES FOR FISH OF DIFFERENT LENGTH GROUPS, SEPTEMBER–NOVEMBER 1954

Figures in italics refer to the most common maturity stage

Length Group	Percentage of Females at Gonad Stage:						No. of Fish
	II	III	IV	V	VI	VII	
September:							
L.C.F. 17–28 cm	20		*70*	10			10
L.C.F. > 28 cm			*38*	24	*38*		21
October:							
L.C.F. 17–28 cm			13	33	*47*	7	15
L.C.F. > 28 cm				33	*50*	17	6
November:							
L.C.F. 17–28 cm	11		*45*	28	11	5	18
L.C.F. > 28 cm			13	36	*45*	6	31

(ii) *Size and Age at First Maturity.*—The smallest running ripe female was only 21·6 cm in L.C.F.; this was probably exceptional, since the next smallest with streaming ova was 25·0 cm. Females in group III, including fish which had only just completed their second year of life, had running ripe ovaries. Many, however, showed no signs of ovarian maturation and it was unlikely that they would spawn before the next season. Table 2 depicts the occurrence of gonad stages throughout the whole of the breeding season. It is obvious that group II fish do not spawn; a few group III fish attain full maturity but the majority do not develop beyond stage IV or V; while it appears that all older fish will participate in breeding activities during the current season.

For males the data are fewer and it is possible only to mention the size at which sexual maturity first becomes apparent. A running ripe male of 26·0 cm

was the smallest in which this feature became obvious. Maturation stages III to VI were observed in fish of L.C.F. 25·0 cm or more, with only three exceptions. The conclusion is that a few males probably attain sexual maturity at the end of 2 years, but all are mature at 3 years.

TABLE 2

GONAD MATURITY STAGES OF FEMALES THROUGHOUT THE SPAWNING SEASON FOR EACH AGE GROUP

Figures in italics refer to the most common maturity stage in each group

Age Group	Percentage of Females at Gonad Stage:								No. of Fish
	I	II	III	IV	V	VI	VII	VIII	
I		*75*	12·5	12·5					16
II		4·5	4·5	31	*34*	17	6	3	90
III			1·5	13	*32·5*	*32·5*	7·5	13	68
IV				4	*40*	*40*	4	12	25
V					33	*34*	33		3
VI					*50*	*50*			2

(iii) *Spawning Habits in the Different Regions.*— pawning times in the Port Lincoln area and over the whole of Spencer Gulf coincided and no differences were noted between the fish from these regions. Between the Port Lincoln and Gulf

TABLE 3

GONAD MATURITY STAGES IN SEPTEMBER FOR FEMALES IN PORT LINCOLN AND PORT WAKEFIELD AREAS

Port Lincoln figures are for 1954 and Port Wakefield figures for 1955. Figures in italics refer to the most common maturity stage in each group

Length Group	Percentage of Females at Gonad Stage:								No. of Fish
	I	II	III	IV	V	VI	VII	VIII	
Port Lincoln area:									
L.C.F. 17–28 cm		*50*	22	28					32
L.C.F. > 28 cm		6	*78*	14·5	1·5				64
Port Wakefield area:									
L.C.F. 17–28 cm				*70*	10				10
L.C.F. > 28 cm				*38*	24	*38*			15

St. Vincent fish there did appear to be some slight variation. The occurrence of macroscopic gonad stages during September of 1954 and 1955 differed for these two regions in so far as data collected during two different years can be accepted for comparison (Table 3). In both young and old spawning fish, i.e. 28·0 cm or

less and greater than 28·0 cm respectively, the Gulf St. Vincent garfish showed a more advanced state of gonad development than did those from Port Lincoln. Furthermore, spawning and spent fish persisted later in Gulf St. Vincent material than in fish from Spencer Gulf including the Port Lincoln fish. Notwithstanding the appearance of the first ripe female among Port Lincoln and Gulf St. Vincent fish respectively on almost the same day in September of both 1954 and 1955, gonads of the majority of Gulf St. Vincent females are the more advanced; though the time difference is probably small.

Temperature is often responsible for fixing spawning times, the effect being noticeable as a north–south gradient; i.e. the spawning period varies according to the latitude (Fairbridge 1951). In more northerly and tropical waters, summer spawning usually takes place earlier in the season than it does further south, where breeding begins as the seas become warmer. A more protracted breeding season is also a feature of warmer-water fish. The waters at the head of Gulf St. Vincent are appreciably warmer in early summer than the more oceanic water bathing the Port Lincoln area. Thus the garfish appears to conform to the general principle of higher water temperature causing accelerated gonad development.

IV. Age Determination in Garfish by Means of Otoliths

(*a*) *Methods*

The sea garfish loses its scales very readily when handled, so that most of the market samples were almost scaleless except for a small region just behind and on either side of the dorsal fin. Scales from this area on a number of fish were collected and examined, but annuli were very indistinct and the scale method was abandoned for age studies. Otoliths, however, did provide a possible means for telling the age of the sea garfish. In addition, the length measurements of many fish were analysed by Petersen's method of length frequency polygons as a further check on age groups. Otoliths were removed from every fish used in gonad studies, and special otolith samples were also collected from males and females during the recording of length frequencies. In all, about 2200 otoliths were read as part of the age and growth rate study.

To extract the otoliths a transverse cut was made on the dorsal surface of the head just behind the posterior rim of the eye. By bending the head downwards about this incision it snapped open and the otoliths could usually be seen in their chamber, from which they were easily removed with fine forceps. This method proved quick and simple; about 150 fish could be dealt with in an hour. Both otoliths were collected from fish used in gonad studies; only the right otolith was taken from other fish. The otoliths were stored dry in numbered pence envelopes. Instead of collection data being recorded on the envelopes a code system of numbering was followed, to remove the possibility of bias in reading otoliths of known origin.

With regard to storing otoliths, some workers have stressed the importance of not allowing them to become dry while others took no such precautions. It is possible that larger otoliths are more affected by drying than small ones. The large otoliths of the hake become opaque if dry, while smaller plaice otoliths do not lose their clarity. That the legibility of garfish otoliths did not suffer from the effects of drying

is shown by the fact that, in repeating the readings almost a year later, no diminution in the clarity of otoliths was noticed during the second reading.

Dakin (1939) carefully ground his flathead otoliths in order to bring out the rings more clearly. Such preparation was not carried out on garfish otoliths before they were examined. To read the otoliths, they were placed in a black dish (a bakelite cap) containing water to a depth of about 5 mm. A thin beam of light was focused behind the otoliths. Readings were made with the naked eye (cf. Hickling 1933; Bowers 1954) except where a hand lens was used to distinguish closely set marginal bands in advanced age groups. All readings were carried out by the author. Otoliths ranged in length from 2·5 to 8·0 mm along the long axis and were up to 1·0 mm thick.

(*b*) *The Otolith as an Index of Age*

For the otolith to be useful in deciding the age of the garfish it must retain some mark or structure which forms at regular intervals (preferably once a year).

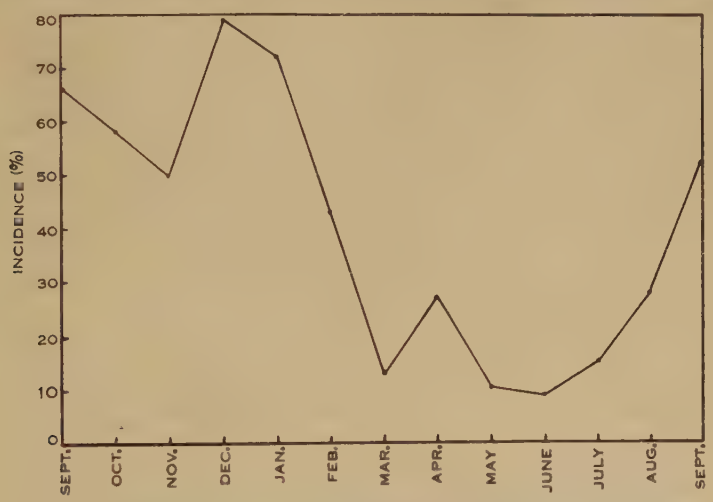

Fig. 11.—Monthly percentage incidence of opaque otolith margins for the 13-month period September 1954 to September 1955.

The deposition of translucent and opaque zones in otoliths can be studied over a period in order to determine when these structures are laid down. Since the otolith bands are formed as a result of regular concretions, the alternate opaque and translucent zones must at some stage actually constitute the otolith margin. If the occurrence of opaque margins is plotted as a percentage of all otoliths examined during each month of the year it should be possible to find the time at which the opaque zones are developed. This has been done for the period September 1954 to September 1955, and the results are shown graphically in Figure 11. The otoliths were examined without knowledge of their date of collection. They were classified as having an opaque or a translucent margin; transitional or doubtful otoliths were discarded.

It is clear that most otoliths had translucent margins in June and opaque margins in December. The formation of a supernumerary translucent zone is

suggested by a low percentage of opaque zones in March. Once a year—in early summer—the opaque zones are laid down in the otolith of the garfish; while the translucent bands are deposited during the winter months. Molander (1947) observed a similar condition in the plaice, which deposited translucent otolith zones in the autumn–winter period and the opaque zones during spring and early summer. This suggests that some seasonal effect may induce these differential depositions. Thomson (1951) has shown that the annuli in the scales of sea mullet from Western Australia were formed in September or October. The annulus marked the end of a period of almost no growth at the time of lowest water temperatures, and there was also some degree of correlation between sea temperatures and growth. Rapid growth of the fish is indicated by deposition of the opaque bands, while slower growth is reflected in translucent bands or annuli (see Hickling 1931; Gross 1947; Molander 1947). However, there are no data to prove conclusively that growth in the garfish ceases or is slowed during winter, so that the meaning of the alternate translucent and opaque bands cannot be determined with certainty. Only a few other age studies using otoliths have been carried out in Australia; and the basic findings were the same as those for the garfish. The annuli were formed in the tiger flathead and spotted whiting during the winter months, and the opaque zones in summer (Dakin 1939; Fairbridge 1951; T. D. Scott 1954). These so-called "winter rings" could well be induced by the lower sea temperatures at the time of their formation. Changes in condition of the hake throughout the year were consistent with the seasonal activities of that fish, activities which again were reflected in the otolith (Hickling 1933). The greatest growth rate and the highest condition of the fish occurred in spring and coincided with maximum incidence of opaque otolith margins, while autumn fish were in poor condition and possessed otoliths with translucent margins at a time when growth was minimal. For the purpose of this paper it will therefore be assumed that factors which operate on the formation of otolith bands in other fish are similarly effective in the South Australian sea garfish.

Hickling (1933) counted the opaque zones of his hake otoliths and assigned the fish to year groups according to the number of these bands, because the translucent annulus which followed came at the end of a completed year. In the garfish an annulus is laid down around an opaque nucleus after about the first 6 months of life and at the end of the first year the first opaque *band* is formed. Thus the number of opaque bands represents the actual age of the garfish in years. However, the date at which the annulus forms is usually accepted as the "arbitrary birthday", notwithstanding the fact that this may occur at the expiration of an incomplete period of years. For example, Fairbridge (1951) recognized this fact in the tiger flathead, which spawns in summer and deposits an annulus in winter similar to that of the garfish. The age groups are denoted as the 0, I, II groups, etc.: until one annulus is present the fish belongs to the 0 group, the I group has one annulus, the II group has two annuli, and so on. These groups are respectively aged about 6, 18, and 30 months, etc.

The number of opaque zones, including the central nuclear region, clearly marked off by a subsequent translucent annulus will indicate the age group to which a garfish belongs. This procedure is followed for the remainder of the paper. However, when reference is made to, say, a 1-year-old or a 2-year-old fish, this

implies the actual age in years. As experience led to greater confidence in otolith readings the interpretation became more certain. The true bands were noted and supernumerary annuli allowed for after clearly defined otoliths had been compared with confused ones. This was especially necessary in otoliths with obscure central regions. However, it is probable that perfection was still not achieved in all otolith readings, so that some erroneous or dubious results may yet be present.

(c) *The Validity of the Otolith Method*

Graham (1929) adduces much evidence showing why caution should be exercised in age and growth rate studies based on scale or otolith readings. Before otoliths of the sea garfish can finally be accepted as a means of age determination evidence should be presented to verify the method.

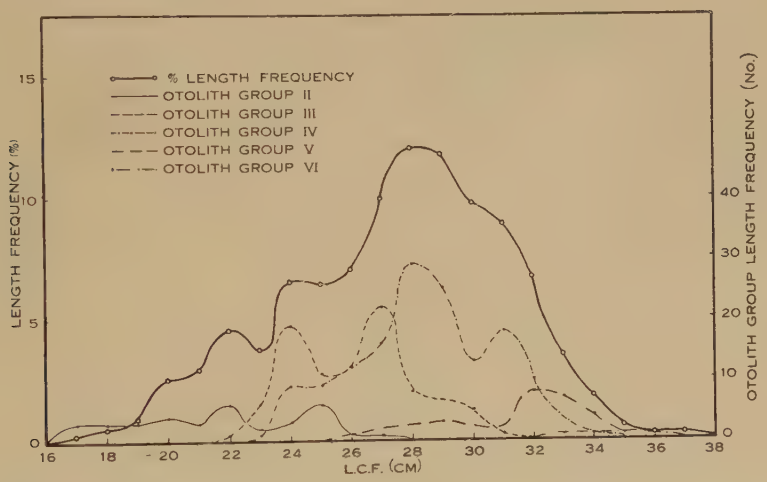

Fig. 12.—Length frequencies compared with length frequency curves of separated age groups arrived at by the otolith method. Data for garfish taken in Port Lincoln region, May and June 1955.

Five tests for the validity of the scale method were put forward by Graham in his classical paper:

(i) Agreement with Petersen's method.

(ii) The seasonal record.

(iii) Observation of the stock over a period of years; and "marked" scales.

(iv) Marking experiments.

(v) Tank or pond experiments on fish of known age.

Tests (i) and (ii) are immediately applicable; but test (iii) can only be made after data have been collected for a number of years. No experiments after the style of tests (iv) and (v) have been attempted.

(i) *Agreement with Petersen's Method.*—When the lengths of a sample of fish are measured and then plotted as a frequency distribution, modes or peaks should

occur at the approximate mean lengths of each year class. In the earlier years the successive modes should be more widely spaced than those of the older age groups, on account of the slowing down in the growth rate. Modes should also be obvious at about the mean length of each age group as determined by otolith readings.

Figure 12 is a graphical portrayal of the length frequency distribution of sea garfish from the Port Lincoln region for the bimonthly period May–June 1955. Modes are obvious in the length frequency polygon at 20, 22, 24, 28, and (probably) 31 cm. The length frequency curves for separate otolith groups of fish collected during the same months are also depicted as smaller polygons. Each of the curves displays more than one mode in all except group IV. The third mode in group II corresponds with a mode in group III and possibly even in group IV, and modes

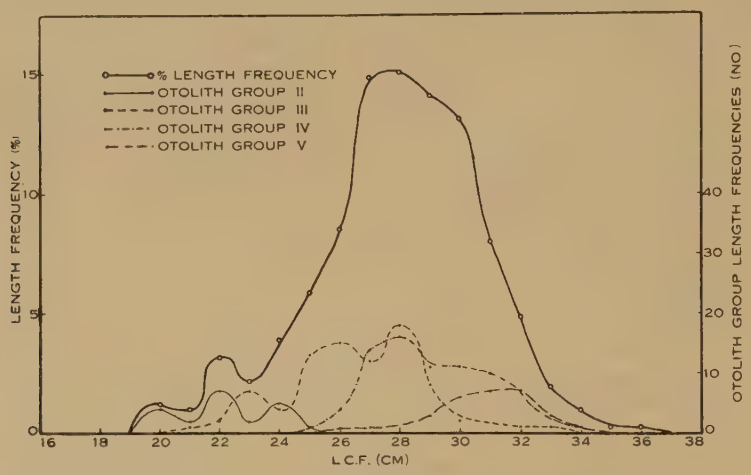

Fig. 13.—Length frequencies compared with length frequency curves of separated age groups arrived at by the otolith method. Data for garfish taken in Spencer Gulf region, June and July 1955.

in other curves also coincide with one another. In spite of the double check when examining otoliths, faulty interpretation or failure to recognize supernumerary annuli may explain the anomalous results. The multimodal curves for the younger age groups could be produced by the presence of early- and late-spawned fish whose actual ages might differ by almost 6 months. The annuli and opaque bands on older otoliths are so close that, despite caution, some errors may have arisen; in any case lengths tend to merge in the older age groups, for which reason Petersen's method is not accurate when applied to fish of advanced age.

The second mode in the zone III otolith group probably represents group IV fish incorrectly assigned to group III. Similarly the modes at 24 and 31 cm in the group IV polygon are likely to result from wrongly interpreted fish of groups III and V respectively. If these explanations are valid, then peaks in otolith group length frequency polygons occur at 22, 24, 28, 32, and 34 cm in groups II, III, IV, V, and VI respectively, which is in fair agreement with the modes on the total length frequency polygon.

Similar treatment of material from the Spencer Gulf region for the two months June and July 1955 reveals modal points on the total length frequency curve at 20 (?), 22, 28, and 30 cm (Fig. 13). The first two modes of the group II curve closely approximate those in the total length frequency distribution, while the third peak corresponds with a trough in the group III curve, suggesting that it reflects wrongly grouped fish, i.e. group II instead of group III. Absence of a mode in the length frequency curve between 22 and 28 cm may imply that an insufficient number of fish was sampled so that the true age composition is also obscured. The 28 cm mode for group IV appears to be correctly placed, and is in agreement with a peak on the length frequency polygon; while the spread of the group III curve round 26 cm suggests this to be the modal point for group III fish. Modes in otolith groups, therefore, are present at 20, 22, 26, 28, and 31 cm, which again roughly conforms with Petersen's distribution.

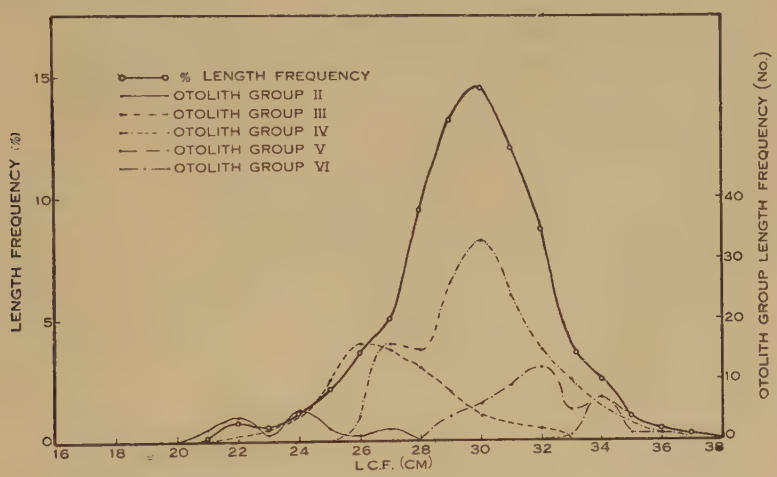

Fig. 14.—Length frequencies compared with length frequency curves of separated age groups arrived at by the otolith method. Data for garfish taken in Gulf St. Vincent region, August and September 1955.

An almost unimodal length frequency polygon for the Gulf St. Vincent fish (Fig. 14) is very likely brought about by the presence of greater numbers of large fish in samples from that region than from elsewhere. Whereas only 60 per cent. of the garfish in Port Lincoln and Spencer Gulf material are 28 cm or more, of the Gulf St. Vincent fish over 80 per cent. are in this category. Among these large fish there is not likely to be a clear-cut age representation on the basis of length, so that modes are almost absent or at best indistinct. They may be indicated at 22, 26(?), 30, 32(?), and 34(?) cm, with which lengths the modal points on the otolith group polygons correspond after allowing for misreading. The bimodal group II polygon is held to represent two stocks spawned at different times, one early and the other late in the season.

(ii) *The Seasonal Record.*—Should it be demonstrated that any one kind of otolith margin occurs only once a year, then the hypothesis that the otolith bands are in fact annual bands is supported. This evidence is regarded as a good check for

the validity of the otolith method, provided that: (1) "there is a very sharp turn-over from one kind of marginal structure to another"; (2) "the stock is adequately sampled during the period of observation, say one complete year and is found to increase in recorded age by one year only" (Graham 1929, p. 36). In no case reviewed by Graham was there any evidence of condition (1) being fulfilled; nor do the garfish show a sharp change from one structure to the next. As for condition (2), a complete month by month coverage over a whole year was not available for any one of the three regions. However, by comparing separate sets of data it was found that, taking the gap in the record into consideration, no regional differences were obvious. In order to carry out Graham's second test any relevant data were grouped together. From 30 to 460 otoliths were examined each month to determine the presence or absence of opaque margins, and the results are presented in Section IV(*c*). They

TABLE 4

GROWTH RATE BY REGIONS: BASED ON OTOLITH READINGS, 1954–55

Region	Data	Length (cm) of Age Group:*						
		I	II	III	IV	V	VI	VII
				(*a*) *Females*				
Port Lincoln	Range	11–12	17–27	23–32	23–34	27–38	31–38	35–36
	Mean	11·5	22·1	26·5	28·5	31·9	34·7	35·3
	Increase		10·6	4·4	2·0	3·4	2·8	0·6
	No. of fish	2	48	209	236	68	9	3
Spencer Gulf	Range		19–28	21–33	24–34	27–35	32–36	
	Mean	20·0	22·3	26·2	29·9	32·2	34·0	
	Increase		2·3	3·9	3·7	2·3	1·8	
	No. of fish	1	38	145	131	46	10	
Gulf St. Vincent	Range		17–27	22–32	25–36	29–37	33–38	
	Mean		20·6	27·0	30·2	33·1	34·7	
	Increase			6·4	3·2	2·9	1·6	
	No. of fish		56	72	119	51	15	
Baird Bay	Range		21–24	21–29	26–30			
	Mean		22·9	26·8	27·5			
	Increase			3·9	0·7			
	No. of fish		15	23	6			

* Age group determined from otoliths by number of opaque bands, including central nuclear region (see text).

TABLE 4 (*Continued*)

Region	Data	Length (cm) of Age Group:*						
		I	II	III	IV	V	VI	VII
				(*b*) *Males*				
Port Lincoln	Range		18–22	22–29	23–32	26–34		
	Mean		20·4	25·2	27·1	29·3	33·0	
	Increase			4·8	1·9	2·2	3·7	
	No. of fish		10	95	85	24	1	
Spencer Gulf	Range		17–24	19–30	25–32	27–33	30–34	
	Mean		21·3	25·6	28·4	31·0	31·7	
	Increase			4·3	2·8	2·6	0·7	
	No. of fish		10	50	59	23	3	
Gulf St. Vincent	Range	17–26	22–29	25–33	28–34	32–33		
	Mean	20·6	26·0	29·0	30·8	32·5	33·0	
	Increase		5·4	3·0	1·8	1·7	0·5	
	No. of fish	32	38	94	29	2	1	
Baird Bay	Range	21–25	23–29	27–30				
	Mean	22·8	26·3	29·3				
	Increase		3·5	3·0				
	No. of fish	8	16	10				

* Age group determined from otoliths by number of opaque bands, including central nuclear region (see text).

show that the otolith bands may be used as indicators of the age of the garfish provided due allowance is made for the supernumerary annuli.

(iii) *Observation of the Stock over a Period of Years.*—A dominant year class may well be represented in a population of fish over a longer or shorter period as, for instance, the 1904 herring brood which constituted a large proportion of the Norwegian catch for 11 years after it became a dominant group in 1908 (Hjort 1926). In successive years after its first appearance the year class should have shown the addition of one annual zone to its otolith (or scale). By regular sampling it should be possible to obtain the length frequency distributions, modes of which correspond to modes in age groups derived by otolith or scale readings (*vide* Hickling 1933; Fig. 18). The numerical strength of the garfish stocks is such that a year class does not remain dominant over a long period of time. The already indistinct

results of the length frequency method seem also to weigh heavily against this third test. Moreover, data have been collected over too brief a period to be useful. The masking of age groups almost as soon as the fish attain a commercially exploitable size means that the year groups cannot be followed for very many years. A tagging programme would be the most effective solution to this aspect of the problem.

TABLE 5

GROWTH RATE WITHIN THE PORT LINCOLN REGION: COFFIN'S BAY GARFISH SEPARATED FROM PORT LINCOLN GARFISH, 1954–55

Region	Data	Length (cm) of Age Group:						
		I	II	III	IV	V	VI	VII
				(a) Females				
Coffin's Bay	Range	11–12	17–25	23–28	23–32	27–32		
	Mean	11·5	20·4	25·1	27·4	29·0	31·0	
	Increase		8·9	4·7	2·3	1·6	2·0	
	No. of fish	2	25	99	124	19	1	
Port Lincoln	Range		17–27	24–32	25–34	27–38	31–38	35–36
	Mean		22·8	27·7	29·6	33·0	35·1	35·3
	Increase			4·9	1·9	3·4	2·1	0·2
	No. of fish		29	110	112	49	8	3
				(b) Males				
Coffin's Bay	Range			19–22	22–29	23–29	26–29	
	Mean			21·0	24·5	26·1	27·1	
	Increase				3·5	1·6	1·0	
	No. of fish			6	57	52	7	
Port Lincoln	Range			18–21	22–29	25–32	28–34	
	Mean			19·5	26·2	28·6	30·2	33·0
	Increase				6·7	2·4	1·6	2·8
	No. of fish			4	38	33	17	1

V. GROWTH RATE

(a) *Observed Growth Rate*

By means of otoliths the ages of nearly 1900 garfish were derived. These fish represented all three major geographic regions, and the results obtained are treated separately for each; males and females are also considered apart. In

addition, a small sample of otoliths was examined from Baird Bay, some hundred miles to the west of Coffin's Bay. The size distribution of male and female garfish of each otolith group is shown for fish from Port Lincoln (Appendix I), Spencer Gulf (Appendix II), and Gulf St. Vincent (Appendix III). There is insufficient material to tabulate for Baird Bay, but the mean lengths of each age group for females and males from each of the four regions are shown in Table 4. Mean lengths of garfish from the immediate vicinity of Port Lincoln are compared with similar data for Coffin's Bay and its environs in Table 5. The length frequencies of the otolith groups are tabulated in Appendixes IV (Port Lincoln only) and V (Coffin's Bay).

To test the significance of the differences in mean lengths for males and females, an analysis of variance was carried out on the figures in Table 4, excluding the Baird Bay results. The differences between male and female lengths in group II were not significant, but those for the Port Lincoln and Gulf St. Vincent fish were so in group III. The differences were significant for all three regions in groups IV and V, but were not significant thereafter, doubtless owing to insufficient data. From the third year in life onwards, therefore, female garfish grow more rapidly and to a larger size than males. Save for group IV, there were no significant size differences between females from the Port Lincoln and Spencer Gulf regions. This single difference was due to the influence of Coffin's Bay fish which, when removed from the Port Lincoln data, left a mean length not significantly different from that of the Spencer Gulf fish. Next, the means for Port Lincoln and Spencer Gulf combined were compared with those for Gulf St. Vincent, and significant variation was observed in all but groups III and VI. Applying the same tests to material for male garfish gave no consistent results. The mean lengths of groups II and III were not significantly different, while those for groups IV and V were so. The differences observed between Gulf St. Vincent males and the remainder were not significant. Females, therefore, appear to grow more rapidly in Gulf St. Vincent than in Spencer Gulf, but males are variable.

The small Baird Bay sample provided results comparable with those of other regions, but no tests were performed on these data. The overall size and preponderance of juvenile age groups is a noteworthy feature of the Coffin's Bay garfish.

(*b*) *Application of Petersen's Method*

Because the spawning period for sea garfish in South Australia extends over a period of 4 months or more, clearly defined year classes cannot be expected to show up in length frequency distributions. A further limitation to Petersen's method as applied to sea garfish may result from the relatively slow growth rate already suggested by the otolith method of age determination. A slow growth rate does manifest itself in the closeness of the modal points of the length frequency polygons, as is shown below. It was suggested in Section III(*c*)(ii) that there may be an early- and a late-spawned stock; this was supported by length frequency analyses (see Section IV(*c*)), which in the first year group gave multimodal curves attributable to the slight age difference resulting from variation in dates when spawned. In spite of the rather confusing material, however, Petersen's method does reveal some results which check with those obtained from otolith readings.

Since the study was initiated in April 1954 the lengths of 15,739 fish have been recorded by the celluloid strip method. With the tip of the upper jaw against the zero point, lengths to the caudal fork were pricked off at the rate of about 300 fish per hour. In 1954 over 4000 fish were measured and during 1955 the number was almost 11,700. These came from practically every fishing port in the State where garfish were known to constitute part of the commercial catch. The three

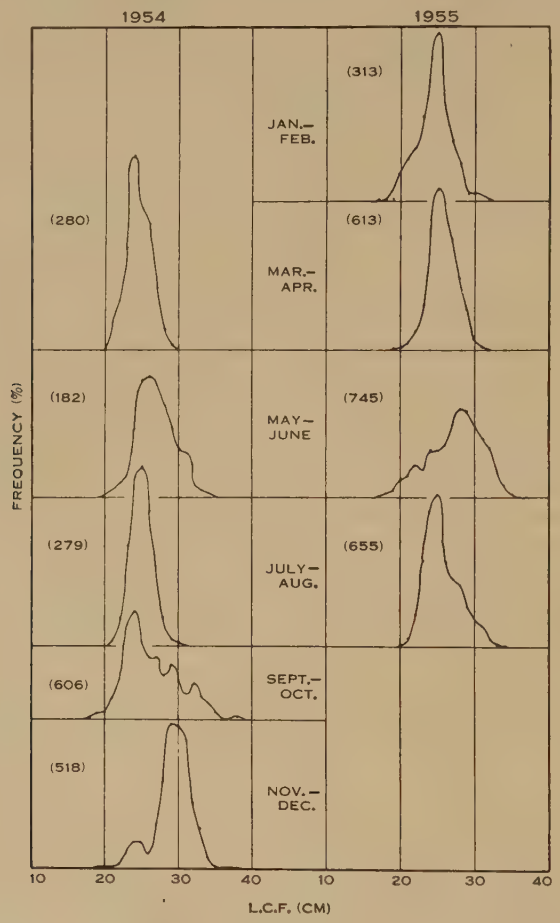

Fig. 15.—Length frequency polygons for the Port Lincoln region at bimonthly intervals from March 1954 to July 1955.

South Australian regions were again treated separately as regards length frequencies. In order to avoid a confused picture resulting from the slow growth rate already indicated, the length frequency polygons were constructed for 2-month periods from April 1954 to December 1955. A greater number of fish were thus included in each polygon; and a wider range of lengths was also available, since many monthly samples showed only slight overlap with one another. The three sets of data are plotted graphically in Figures 15–17.

At best, only rough approximations can be made from the length frequency data. Series of modes are fairly obvious in most of the polygons, but when it comes to following the progress of a certain mode in the course of time, the evidence for modal progression is not very conclusive. In general, the peaks in the curves which are taken to indicate year classes confirm or agree with the findings by the otolith method. Taking October as the time of most intense spawning activity, the September–October curves for 1954 may be said to represent the size frequencies

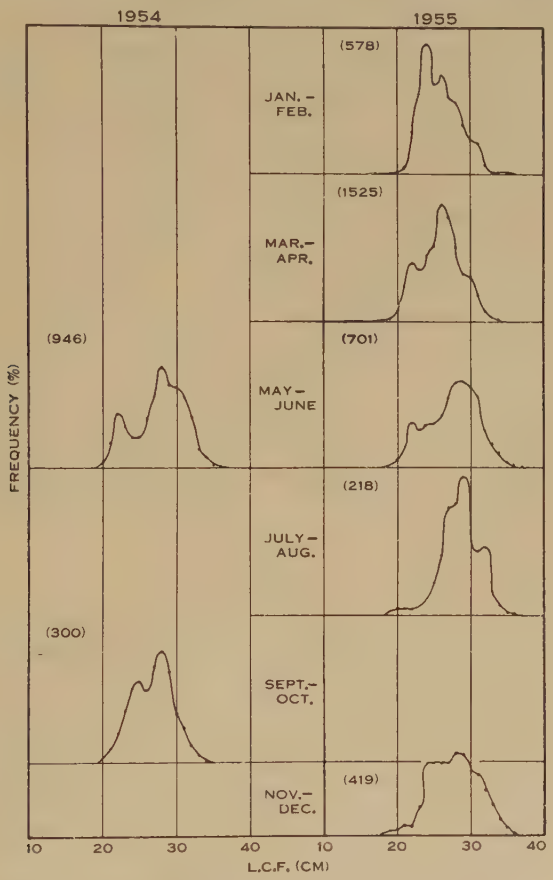

Fig. 16.—Length frequency polygons for the Spencer Gulf region at bimonthly intervals from May 1954 to December 1955.

at the end of one or more complete years in the life of the fish. Definite modes occur in the Port Lincoln data (Fig. 15) for this period at the 24, 27, 29, and 32 cm lengths; and one is also suggested at 19 cm. It is possible that the 24 cm mode can be traced through the year, as it gives way to a 28 cm group at the end of 12 months. Over almost the same period the 29 cm peak gives way to a mode at 31 cm.

All reasoning must be very subjective, since without a previous knowledge of where to expect age groups to occur, it is unsafe to attempt to do more than

distinguish modes on the curves. However, used conjointly with the otolith method, Petersen's method of age analysis by length frequencies does assist in determining the size increase year by year. The periods when slow growth and more rapid growth take place cannot be found simply by inspecting the progression of modes and noting the stage at which this steepens. Since in the later year groups (from III onwards) the length increases by only 2 or 3 cm in a year, the acceleration of growth does not manifest itself in a sudden shift of the modes. The latter are close together, and when any variation in size distribution occurs the displacement of a

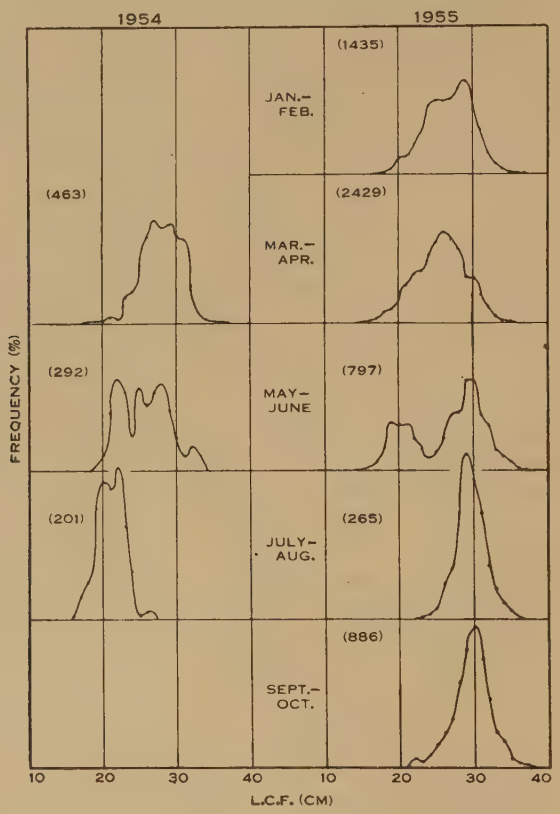

Fig. 17.—Length frequency polygons for the Gulf St. Vincent region at bimonthly intervals from March 1954 to September 1955.

mode by even a centimetre leads to anomalous or confusing results. For this reason clear series of gradual changes in position of modes (reflected by a movement towards the right) are not apparent in the above data. Very similar results and conclusions are to be obtained from a study of the length frequency curves for Spencer Gulf (Fig. 16) and Gulf St. Vincent (Fig. 17) material. Throughout the data individual polygons can be subdivided into peaks which are taken to represent year groups; but the picture is somewhat confused.

From length frequency polygons, then, an approximate idea of the size and age composition of a garfish sample may be obtained. In the discussion of the actual

conditions of the fishery presented in Section VI, the principles and results of the application of Petersen's method and the otolith method of age determination are again followed.

(c) *Otolith Length/Fish Length Ratio*

Being unable to obtain sufficient numbers of juvenile hake for derivation of the mean lengths of these younger age groups, Hickling (1933) resorted to the method of "back-calculation". Whereas calculated growth rates are frequently derived from scale measurements by fishery biologists, the use of otoliths for such a purpose is not widely practised. Hickling's work is the classical example; Fairbridge (1951) arrived at calculated intermediate lengths of New South Wales tiger flathead; and the growth rates of the arctic char and yellowtail flounder were also calculated from measurements made on otoliths (Grainger 1953; D. M. Scott 1954).

Since this investigation of the sea garfish is based upon material almost entirely of market size, small fish, i.e. those less than the minimum legal size, were few in number. Hence it was hoped to arrive at the intermediate lengths of small garfish by calculations from measurements on otoliths. The method of back-calculation depends on the premise that growth in fish length is proportional to growth in otolith length. It has already been shown that the concentric structures in the otoliths are in fact annual bands of growth; and for calculated intermediate lengths to be determined, the exact relation between the diameter of these growth rings and the length of the fish must be established. The ideal equation is

$$l = \frac{L}{V} \times v,$$

where l is the intermediate length, v the diameter of the annulus, L the fish length, and V the otolith length.

The lengths of 511 garfish were classified into average values for each half-centimetre group such that the 20 cm group included fish from 19·8 to 20·2 cm in length, fish 20·3 to 20·7 cm long comprised the 20·5 cm group, etc. Otolith lengths were measured along the long axis by means of a micrometer eyepiece in a low power binocular microscope, and the mean otolith length for each half-centimetre fish group was also calculated. These two values were plotted against one another over the whole size range and a linear relation was obtained. By means of the method of least squares the line of best fit was applied to the parameters (Fig. 18). There were few data for fish less than 17 cm in length, so that the otolith length/fish length relation cannot be accurately assessed. Extrapolation leads to an absurd result where a fish of no length has an otolith almost 1 mm long. There are indications from the only otolith measurement for fish of less than 17·0 cm L.C.F. that the curve does in fact steepen at the smaller values of L and V, showing the otolith to increase in length at a more rapid rate relative to the fish length. This agrees with Fairbridge's (1951) conclusion that growth of the otolith becomes isauxetic above a fish length of 10 cm. Just where this condition arises in the garfish cannot be determined, owing to the gap in the material for very small fish. Extrapolation can be carried out only with caution where actual measurements are not available

to substantiate the calculated relationship. In this case, and in the absence of further data on garfish otoliths, an approximation must be made in order to determine the intermediate lengths of juveniles.

(*d*) *Calculated Intermediate Lengths*

Taking all measurements on fish above 17·0 cm to be valid, and assuming similar validity for the parameters of the two smaller fish, the straight line has

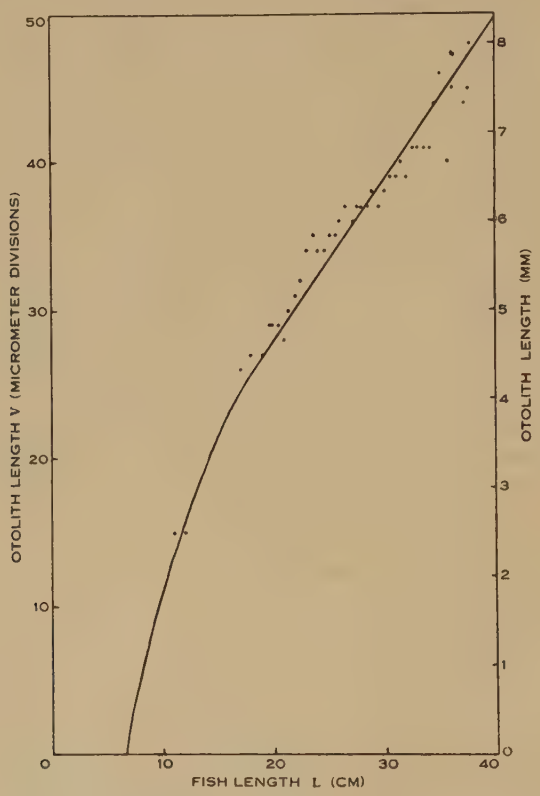

Fig. 18.—Regression of otolith length V on fish length L. Straight line fitted by least squares method; curve produced freehand. Each parameter represents average values of V and L for each 0·5 cm group.

been produced as a freehand curve to the fish length axis. From this curve intermediate lengths have been arrived at for mean values of v_1, v_2, etc., where v is the intermediate length of the otolith to the centre of each annulus.

All fish were caught in the Port Lincoln region only, for which Table 6 summarizes the results. As already noted in dealing with the mean lengths of age groups, the intermediate lengths of females become significantly greater than the

corresponding male lengths after the second year; the ultimate size relation between the sexes cannot be found as insufficient data are available.

(e) *Length/Weight Relationship*

Changes in weight of the garfish as its length increases are useful to the fishery biologist, and are a further aspect of the study of the growth rate. Generally weight is a function of length and may be expressed by the equation

$$W = cL^n, \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where W is the weight, L is the length, and c and n are constants.

When

$$W = KL^3, \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

K is referred to as the ponderal index or condition factor, and is used for comparing

TABLE 6

SUMMARY OF CALCULATED INTERMEDIATE LENGTH DATA FOR THE PORT LINCOLN REGION, 1954–55

Fish Length Group	No. of Readings	Otolith Length v (micrometer divisions)		Fish Length (cm)	
		Range	Mean	Range	Mean
		(a) Females			
l_1	307	5–20	11·5	6·7–13·8	9·3
l_2	258	14–32	24·0	10·4–23·8	16·7
l_3	139	25–35	30·5	16·9–26·6	22·5
l_4	41	31–40	36·3	22·8–31·2	27·8
l_5	5	38–44	41·2	29·3–34·8	32·2
l_6	1	41	41·0		32·1
		(b) Males			
l_1	94	6–19	12·2	7·2–13·3	9·7
l_2	75	17–29	23·5	12·2–21·2	16·3
l_3	34	23–35	30·4	15·8–26·6	22·4
l_4	6	34–38	35·2	25·7–29·3	26·7
l_5	1	42	42·0		33·0

fish from time to time when the weight bears a seasonal relation to the length (cf. Hickling 1930). In the present study, equation (1) above is used in its logarithmic form, i.e.

$$\log W = \log c + n \log L.$$

The fork length and weight in grams of 431 females and 191 males were measured on whole fish, i.e. with gut and gonads intact. Only the freshest fish were treated in order to obtain as near to live weights as possible. Weighings were carried out on spring balances reading to the nearest gram for fish up to 100 g and to the

nearest 5 g in larger fish. These lengths and weights were averaged for half-centimetre groups, e.g. the 21 cm group comprised lengths between 20·8 and 21·2 cm, the 21·5 cm group between 21·3 and 21·7 cm, etc. Mean lengths and mean weights for each sex were transformed to logarithms which, plotted graphically, gave a straight-line relation. The lines of best fit, calculated by the method of least squares, are expressed by the equations:

$$\log W = 3{\cdot}1550 \log L - 5{\cdot}7038,$$

for females, and

$$\log W = 3{\cdot}0945 \log L - 5{\cdot}5386,$$

for males. Thus the cubic law is very nearly obeyed, and for all practical purposes it may be stated that the weight of the sea garfish varies as the cube of its fork length. Royce (1942) found that the relation between total length and weight more closely approached the real value than did the standard length/weight ratio. Since the maximum total length has not been recorded in this investigation, factors for conversion to this measurement will have to be calculated and the appropriate adjustments made at a later date.

Steven (1952) obtained a straight-line length/weight relation for the common English mackerel, *Scomber scombrus* Linnaeus, but there was a distinct inflexion in the growth curve, so that two separate lines represented the length/weight ratio of different size groups. Weight increased at a more rapid rate relative to length after a certain size had been reached, and this size corresponded to that at which the fish attained sexual maturity. No such obvious variation in change of weight with length throughout the size range was observed in the sea garfish.

(*f*) *Fork Length and Total Length*

Hile (1948) advocated the adoption of a standardized system of length measurements for all fishery investigations. As a result of Royce's (1942) conclusions, the use of the maximum total length, i.e. from the anterior tip of the snout to the tip of the tail in the direction of the long axis, was suggested as the only length to be used in further work. For the purpose of minimum legal lengths this is already the standard practice, especially among fishermen, who regard the length of a fish as the maximum total length obtainable without actually stretching the fish. Since the original data for this investigation are in metric units in terms of fork length, factors for converting these data into English units in terms of total length are supplied. Hile's paper was not seen until after 1262 natural total lengths and fork lengths had been measured. A maximum difference of half an inch is possible when comparing maximum and natural total lengths, and this is allowed for in the conversion table. Mean values of fork length and natural total length were computed for each half centimetre of fork length, and conversion factors were calculated for each of these pairs of means over the whole size range. A gradual increase in the ratio of total length to fork length was discernible over the range 17–22·5 cm for which figures are to hand. Such a progression was also noted in young fish by Beckman (1948). Above 22·5 cm the ratio was very constant. In any case the variation occurred only in the third place of decimals. The conversion factors are set out in Table 7 for fish below and above 22·5 cm in L.C.F.

(g) *Growth in the Sea Garfish Reviewed*

The sampling technique which utilizes garfish only of minimum legal size or over excludes the smaller fish which might otherwise contribute to the average size of each age group. For this reason the average length-for-age of younger fish would be expected to exceed the calculated intermediate length, which it does. Only when the smaller end of the size range of a particular age group is larger than the minimum legal length can it be concluded that a complete coverage of the age group has been made. The minimum legal length is 8 in., or 20·5 cm, total length, which is equivalent to 19·5 cm L.C.F. Hence age group III is the first which can be said to include all sizes of fish of a given age, so that the mean length should be an accurate figure, as should the mean lengths for all older age groups where a sufficient number of fish have been sampled.

TABLE 7

FACTORS FOR CONVERSION BETWEEN FORK LENGTH (L.C.F.) AND "NATURAL" TOTAL LENGTH (T.L.) FOR SEA GARFISH

Total Length Range (in.)	L.C.F. (cm) to T.L. (in.)	T.L. (in.) to L.C.F. (cm)	No. of Fish
7·0– 9·5	0·415	2·408	104
9·6–15·6	0·417	2·398	1158

It is clear from previous remarks that the calculated intermediate lengths and the mean lengths of age groups are in effect two quite distinct sets of data. The differences between the two series will be clear in earlier age groups where year by year growth is marked, but will become less marked, i.e. approach equality, as growth processes decelerate. This appears to take place in females of group V and possibly in males of group IV, but the paucity of calculated length data for males in group V prevents a conclusion from being drawn.

The progressive length and weight increase during the life of the garfish is shown graphically in Figure 19, where the metric measurements and weights so far used in this report are converted to British units. Since the calculated intermediate lengths apply to fish at a fairly restricted time of the year, these figures are used up to the point where they are no longer accurate, i.e. to the fourth year. Thus the weights are those for fish of intermediate lengths l_1, l_2, l_3, and l_4 of groups I, II, III, and IV respectively. From then on the weights for mean lengths at the end of 4, 5, and 6 years are plotted to give the absolute growth curve. Despite the significant difference in lengths-for-age between males and females of advanced age, there is no departure from a single growth curve by either of the sexes in so far as the scale allows. The positions of the points on the curve reveal a slightly larger weight increase per unit length in the males. However, females attain a

greater age and size, which is a commonly observed feature of fish. The growth rate is uniform during the early years of life, but at about the time of sexual maturity the variation between the sexes becomes manifest. This variation is so slight that no inflexion became obvious in the logarithmic straight-line relation (cf. Steven 1952).

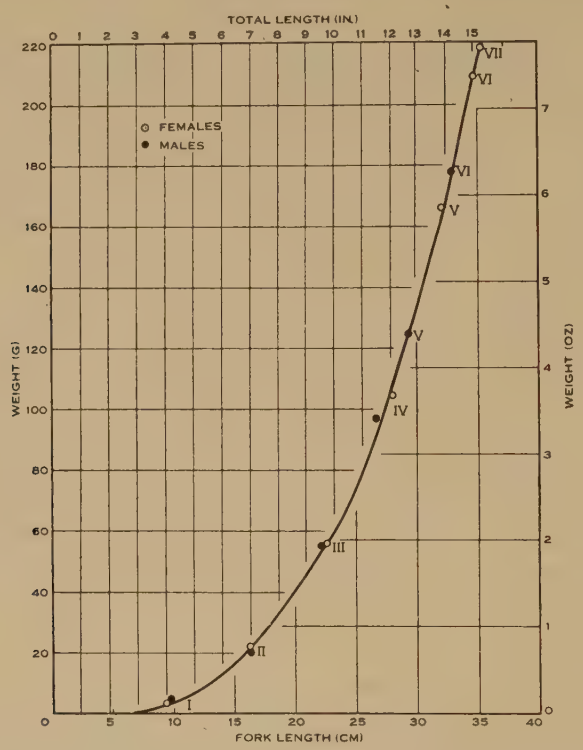

Fig. 19.—Combined growth curve for female and male garfish, converting fork length in centimetres to total length in inches, and weight in grams to weight in ounces. Points represent age groups I–VII.

VI. Management of the Fishery

The possible application of the foregoing results to the commercial fishery for sea garfish in South Australia may now be discussed. In Section III(*d*)(ii) the size at which female garfish become sexually mature was shown to lie at around 25 cm L.C.F. or about 11 in. T.L. It was found too that some 2-year-old fish were mature and had ripe roes during the breeding season, but all 3-year-old fish were judged to be sexually mature at the breeding period. The mean size of a group III female garfish is 27·5 cm L.C.F. or 12 in. T.L., so that the 25 cm fish, participating in their first spawning activities, would be just approaching the end of their third year of life. A fish 8 in. in T.L. has an L.C.F. of about 19 cm, i.e. it is approaching the end of its second year. Thus many garfish are subjected to at least one year's fishing before they have spawned once.

Analysing the catch by months, the average weight per month passing through the Adelaide market has been determined for the 10-year period 1936–37 to 1945–46, and a graphical illustration of the trend is shown in Figure 20. The yearly totals were "raised" to equality, in order to make the monthly averages comparable. It is clear that the fish are least abundant in November, the amounts present in October and December also being small. This period coincides with the breeding season and it would appear, therefore, that the fish are not so heavily fished at this time as, for instance, during the autumn months. Hence spawning fish are naturally protected by virtue of what appears to be a movement away from the fishing area.

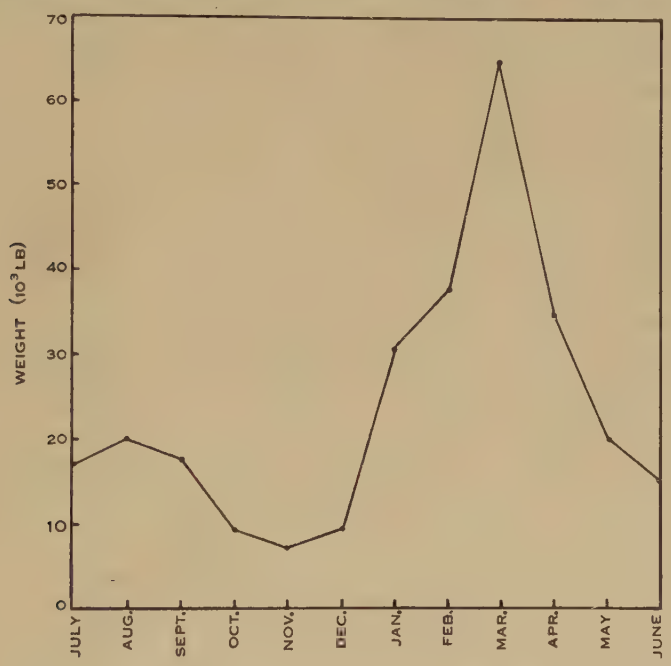

Fig. 20.—Average monthly weight of garfish handled in the Adelaide market during the 10-year period 1936–37 to 1945–46.

This corroborates statements by fishermen, who believe that garfish spawn in open water or tidal runs; but is contrary to the previous observation (Section III(*d*)(i)) that spawning occurred over *Zostera*-covered flats. While these facts refer to fish in the Adelaide market where Port Lincoln fish occur only spasmodically, it is known that the abundance of garfish in the Port Lincoln market follows the pattern shown at Adelaide; netting is most actively pursued during the winter months. However, there are no production figures to bear out this observation; but in spite of this deficiency the Port Lincoln fishery may be examined in the light of Adelaide market findings. These returns show that spawning fish are not subjected to intensive fishing for some reason or other, of which the non-availability due to emigration may be one. During most of the year small garfish are available and are caught along with larger fish.

The age and size at which a fish becomes sexually mature are not now generally regarded by fishery biologists as the criteria upon which the minimum legal length should be based. The theoretical ideal as regards management of a fishery lies in the principle that the mortality due to fishing intensity should be balanced by annual recruitments over and above those required to offset natural mortality. Since the number of eggs produced by the common commercial species of fish is measured in many thousands, or even millions, a relatively few spawning individuals can maintain the species; only a small fraction of a new generation from a large spawning stock need survive to produce the same result. If the weight of fish removed from a certain year class can be replaced by the developing young fish by the time the latter attain this age, then survival of the species is assured, but the fishery may be said to be most productive only when the maximum growth in terms of weight coincides with a minimum mortality rate.

Whether the above conditions exist in the South Australian fishery for garfish cannot be determined yet on account of the present lack of sufficient data, both biological and statistical, upon which to work. The foregoing remarks do serve to emphasize future lines of investigation as a basis for sound fishery management. A study of the fecundity of the garfish is required, along with observations on the survival of fry and small immature fish. It is known from macroscopic examinations and a very few fecundity estimations (Ling, unpublished data) that the number of eggs spawned is relatively small—about 9000–10,000—the eggs themselves being so large. Catch analyses year by year in terms of age composition should reveal the progressive year class strength subject to the effect of fishing. Catch and fishing effort statistics are therefore very necessary before a full management programme can be contemplated. Examples of possible overfishing and optimum fishing are manifest in the Coffin's Bay and Gulf St. Vincent age compositions as revealed by otolith groups. Rapid growth in Gulf St. Vincent fish to an age 1 year less than that observed in Port Lincoln samples, with the size composition in favour of larger fish, suggests that either the rate of removal of the species is such as to allow fast growth and subsequent replacement by weight of fishable material, or unusually good feeding grounds exist at the head of Gulf St. Vincent. Fishing activity in Coffin's Bay tends to keep the already small-sized young fish very much in the majority. Unduly heavy exploitation of an adult fish population has not been clearly revealed in the present investigation, so that the comparison between Gulf St. Vincent and Coffin's Bay garfish cannot be pressed too far.

The only reason for an adjustment in the minimum legal length of the garfish for the present is really an economic one, although the fish are not sexually mature when the legal size is reached. All fish which survive from the second year to the third, when the majority are sexually ripe for the first time, undergo a 100 per cent. increase in weight. The marketable value of "size" garfish is already criticized by works managers. Since most of the fish are filleted, there is a larger percentage of waste from the smaller than from the bigger fish; furthermore, the filleting operation is simpler on a larger fish than on a small one. Medium and large sizes (from 12 in. in T.L.) are the popular ones for fish purchased in the round by householders.

The universally recognized position with regard to Australian fisheries in general is a realization that the stocks are not over-abundant (see Thompson 1943).

Thus strict conservation measures at the outset may be justified by later studies; or if this is not so, changes can be made in the light of added knowledge. There is insufficient evidence on brood strength and mortality rate in the garfish to justify a change in legal length for the preservation of non-spawners. The absence of catch statistics going back over a long period of time does not allow the overall trend in garfish populations to be observed, and no check on the effects of a size increase would be possible. It has already been shown that increasing the minimum legal length of sea and yellow-eye mullet has had little effect on the respective fisheries, and these changes were instituted on the basis of far more knowledge than is to hand concerning the garfish (Thomson 1950, 1956).

By studying length frequencies over a period of time it was possible to arrive at the approximate length composition of all garfish sampled at Port Lincoln, 4100 in all. The proportion of fish below 25 cm in L.C.F. to those above this length varied from 8 to 71 per cent., with an overall average figure of 47 per cent. or nearly half. While all Port Lincoln regional samples are not divisible into those from Coffin's Bay or the Port Lincoln area in particular, the few definitely known to be Coffin's Bay lots include a high percentage (up to 70 per cent.) of fish below 25 cm in L.C.F. Moreover the few samples from outside Coffin's Bay show a preponderance of the larger category. That the garfish population in Coffin's Bay is of a juvenile constitution seems fairly obvious on the basis of size, although it could be a population of stunted old fish. However, the age analysis of Coffin's Bay and Port Lincoln fish separately shows that the former are indeed young in age composition, while the full scale of ages shows up in Port Lincoln material. Table 5 (Section V(*a*)) summarized these data. That the fish probably belong to the same stock can be shown by comparing certain meristic features and morphometric measurements. Whereas there are significant differences between such counts and measurements for other localities when compared with those for Port Lincoln, those for Coffin's Bay almost coincide, which suggests a common origin in so far as spawning place is concerned (Ling, unpublished data).

The relation of the Coffin's Bay garfish to the rest of the Port Lincoln regional stock is clearly one of close affinity, in spite of the spatial separation of 120 sea miles. These fish present an example of either a developing young population or one subjected to intensive fishing. Heavy fishing by week-end netters does take place in Coffin's Bay which, however, does not receive so much attention from full-time professional fishermen. The relatively small return is not sufficient inducement for these men to exploit the large numbers of small garfish (and, incidentally, other species including whiting and ruff). Either of the above causes of a predominantly juvenile stock of garfish justify the recommendation that this species should not be netted in Coffin's Bay at any time of the year.

VII. Acknowledgments

Financial support for this investigation came from the Research Grants Committee of the University of Adelaide, to whom the author expresses his gratitude. The project was suggested and in a large measure guided by Mr. W. B. Malcolm of the Division of Fisheries and Oceanography, C.S.I.R.O. Dr. J. M. Thomson,

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Appendix I

Number of Garfish of each Centimetre Group Arranged in Otolith Groups, Port Lincoln Region

L.C.F. (cm)	Females (575 examined) Opaque Zones							Males (215 examined) Opaque Zones						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
11	1													
12	1													
13														
14														
15														
16														
17		3												
18		3							1					
19		2							2					
20		5							2					
21		7							2					
22		5							3	3				
23		6	12	2						12	1			
24		6	28	3						21	10			
25		8	33	9						21	11			
26		2	31	26						18	16	3		
27		1	47	45	4					8	10	2		
28			25	44	4					8	15	3		
29			11	38	7					4	11	7		
30			15	23	5						5	2		
31			5	21	8	2					3	2		
32			2	16	10						3	4		
33				6	14	1							1	
34				3	7							1		
35					2	3	2							
36					2	1	1							
37					3									
38					2	2								
Total	2	48	209	236	68	9	3	—	10	95	85	24	1	—

Appendix II

Number of Garfish of each Centimetre Group Arranged in Otolith Groups, Spencer Gulf Region

L.C.F. (cm)	Females (371 examined) Opaque Zones							Males (145 examined) Opaque Zones						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
17									1					
18														
19		1								1				
20	1	6							3	1				
21		5	1						1					
22		12	5						2	1				
23		7	11						1	5				
24		3	18	1					2	6				
25		1	27	1						7	3			
26		2	14	5						12	2			
27			20	15	1					8	10	1		
28		1	28	10						4	18			
29			12	18	2					4	11	2		
30			4	28	2					1	10	5	1	
31			3	24	10						4	6	1	
32			1	18	12	2					1	5		
33			1	8	7	1						4		
34				3	9	3							1	
35					3	3								
36						1								
Total	1	38	145	131	46	10	—	—	10	50	59	23	3	—

Appendix III

Number of Garfish of each Centimetre Group Arranged in Otolith Groups, Gulf St. Vincent

L.C.F. (cm)	Females (313 examined) Opaque Zones							Males (196 examined) Opaque Zones						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
17		3							2					
18		9							6					
19		17							8					
20		7							1					
21		4							2					
22		2	1						5	1				
23		1	3						3	3				
24		4	6						3	1				
25		7	10	2					1	6	1			
26			9	4					1	13	2			
27		2	11	10						8	16			
28			12	8						5	18	1		
29			11	18	1					1	20	5		
30			6	22	1						20	6		
31				22	5						12	7		
32			3	18	14						3	7	1	
33				11	8	3					2	2	1	1
34				3	13	7						1		
35					7	1								
36				1	1	1								
37					1	2								
38						1								
Total	—	56	72	119	51	15	—	—	32	38	94	29	2	1

Appendix IV

Number of Garfish of each Centimetre Group Arranged in Otolith Groups, Port Lincoln only

L.C.F. (cm)	FEMALES (311 examined) Opaque Zones							MALES (93 examined) Opaque Zones						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
17		2												
18		2							1					
19		2							1					
20									1					
21		2							1					
22		2								1				
23		4								1				
24		5	3	1						4				
25		7	10	2						8	2			
26		2	11	7						7	6			
27		1	30	14	1					6	1			
28			23	10						8	5	3		
29			11	15	1					3	8	5		
30			15	19	2						5	2		
31			5	21	6	1					3	2		
32			2	14	9						3	4		
33				6	14	1							1	
34				3	7							1		
35					2	3	2							
36					2	1	1							
37					3									
38					2	2								
Total	—	29	110	112	49	8	3	—	4	38	33	17	1	—

Appendix V

Number of Garfish of each Centimetre Group Arranged in Otolith Groups, Coffin's Bay Region only

L.C.F. (cm)	Females (270 examined) Opaque Zones							Males (122 examined) Opaque Zones						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7
11	1													
12	1													
13														
14														
15														
16														
17		3												
18		3												
19		2							1					
20		5							1					
21		5							1					
22		3							3	2				
23		2	12	2						11	1			
24		1	25	2						17	10			
25		1	23	7						13	9			
26			20	19						11	10	3		
27			17	31	3					2	10	2		
28			2	34	4						11			
29				23	6					1	1	2		
30				4	3									
31					2	1								
32				2	1									
33														
34														
35														
Total	2	25	99	124	19	1	—	—	6	57	52	7	—	—

OBSERVATIONS ON THE BIOLOGY OF THE GREENTAIL PRAWN, *METAPENAEUS MASTERSII* (HASWELL) (CRUSTACEA DECAPODA: PENAEIDAE)

By W. Dall*

[*Manuscript received July* 25, 1957]

Summary

The ecology, growth, and behaviour of *Metapenaeus mastersii* from the Brisbane River, Qld., are described. Postlarval stages were found to favour a warm sheltered locality with abundant algal cover and salinity below 20‰. Salinity tolerance range of all stages was from almost fresh to sea-water, and activity was at a minimum when the average temperature fell to 16°C. Carapace length was found to be as reliable a measure of size as overall length or volume. Progression of the modes of length frequency distributions was unsatisfactory for finding growth rate, but showed a steady downstream movement as growth progressed. From the growth rate of captive prawns, age at sexual maturity was estimated as 12–15 months at 16 mm carapace length (males) and 20 mm (females) (76 and 95 mm overall). Males were less tolerant of low salinity than females, but did not migrate as far downstream. Fertilization occurred in the lower reaches of the Brisbane River, but spawning occurred outside. The length-volume relationship of prawns above 10 mm carapace length (48 mm overall) did not conform to the curve: volume $= k \times (\text{length})^3$. This deviation was interpreted as due to change of growth characteristics during winter. A reversed respiratory current and other adaptations to burying in the mud, and a possible associated diurnal rhythm are described.

I. Introduction

Müller (1864) gave the first indication that the development of Penaeidae was unique amongst the Eudecapoda, and since then many investigators have described the early life history (prior to 1942 listed by Gurney (1939, 1942); since 1942, by Hudinaga (1942); Gurney (1943, 1950); Anderson, King, and Lindner (1949); Menon (1952); Morris and Bennett (1952); and Heegaard (1953)). Little work was done on the postlarval life history and general biology of the family until large-scale commercial fishing was well established. Spaulding (1908) and Viosca (1920) published preliminary accounts of the biology of *Penaeus setiferus* (Linnaeus) from the Gulf of Mexico, but the first substantial investigation was undertaken by Weymouth, Lindner, and Anderson (1933). Since that date there has been a number of investigations of the biology of the commercially important Penaeinae, mostly in North America (Anderson, King, and Lindner 1949; Gunter 1950; Lindner and Anderson 1954, 1956; Hildebrand 1955; Williams 1955*a*, 1955*b*; Johnson and Fielding 1956; and several smaller papers quoted by these authors). Menon (1955) in India, and Hudinaga (1942), Fujinaga (1955), Ikematsu (1955), and Kubo (1955) in Japan have undertaken similar studies.

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In Australia, Dakin (1938, 1940, 1946*a*, 1946*b*) and Morris and Bennett (1952) have investigated the commercially important *Penaeus plebejus* Hess and *Metapenaeus mastersii* (Haswell) (*Metapenaeus* sp. of these authors; see Racek (1955) and Dall (1957) for systematic account). As most of this work concerned larval stages with only brief mention of the subsequent life history, it was decided to investigate the post-planktonic ecology, growth, and behaviour of *Metapenaeus mastersii*. The Brisbane River, with its abundance of postlarval and juvenile stages, provided a convenient area for this work, which was begun in 1952, utilizing field collections and observations in aquaria.

II. Methods

(*a*) *Field Collections*

Initially prawns were collected at Indooroopilly (Fig. 1) with a rectangular brass frame scoop, 36 by 18 in., with a 6 ft handle. Mosquito netting, of mesh diameter approximately 1·2 mm, was used, and found to retain 5 mm postlarvae. Collections with the scoop were made by wading in water 2–3 ft deep and working with the edge of the frame held against the bottom. The same area was covered on each occasion, and the numbers collected thus gave a rough indication of the relative abundance of prawns, though large prawns could escape it more readily than they could a trawl.

From January 1954 a frame trawl was used, of mouth 5 by $1\frac{1}{2}$ ft, made of four lengths of $\frac{1}{2}$-in. (inner diameter) galvanized water piping, and joined at the corners by standard right angle piping unions. Each carried an eyebolt for each warp of the towing bridle. Three-quarter inch fishing net was used, with mosquito netting lining the cod-end. All trawling was done at high water. The trawl could be used quantitatively by covering the same distance at about the same speed for each haul ($\frac{1}{3}$ mile at 2 kt). However, the frequency distributions obtained for the postlarvae and smaller juveniles were similar for both collecting methods (see Section IV). In Bramble Bay (Moreton Bay) in January 1954, the sample was obtained with a small otter trawl. Additional larger prawns were obtained at Indooroopilly in December 1952, with a small seine net.

(*b*) *Aquaria*

Two sizes of aquaria were used, both 12 in. deep, one 12 by 21 in. and the other 21 by 21 in. Estuarine muddy sand was used to cover the bottom. The aquaria were filled with either Moreton Bay or local river water, and aerated either with a porcelain diffuser or by Richardson's (1952) method. The aquaria were kept out of direct sunlight, 6–8 ft from a window facing north-west.

III. Distribution and Environment

(*a*) *Seasonal Occurrence*

M. mastersii of commercial size (60–75 mm length) usually appear in the lower reaches of the Brisbane River and off Bramble Bay (Fig. 1) in September. Abundance increases to a maximum in November–December as the water tempera-

ture rises (Fig. 2), the size range being 75–100 mm. Thereafter there is usually a decline until the seasonal February rains, after which the largest catches are often obtained. From April to May with falling temperature (Fig. 2) numbers decrease, and usually by early June adult prawns are virtually absent. Postlarval and early juvenile prawns favour shallow sheltered localities ("nursery grounds") such as

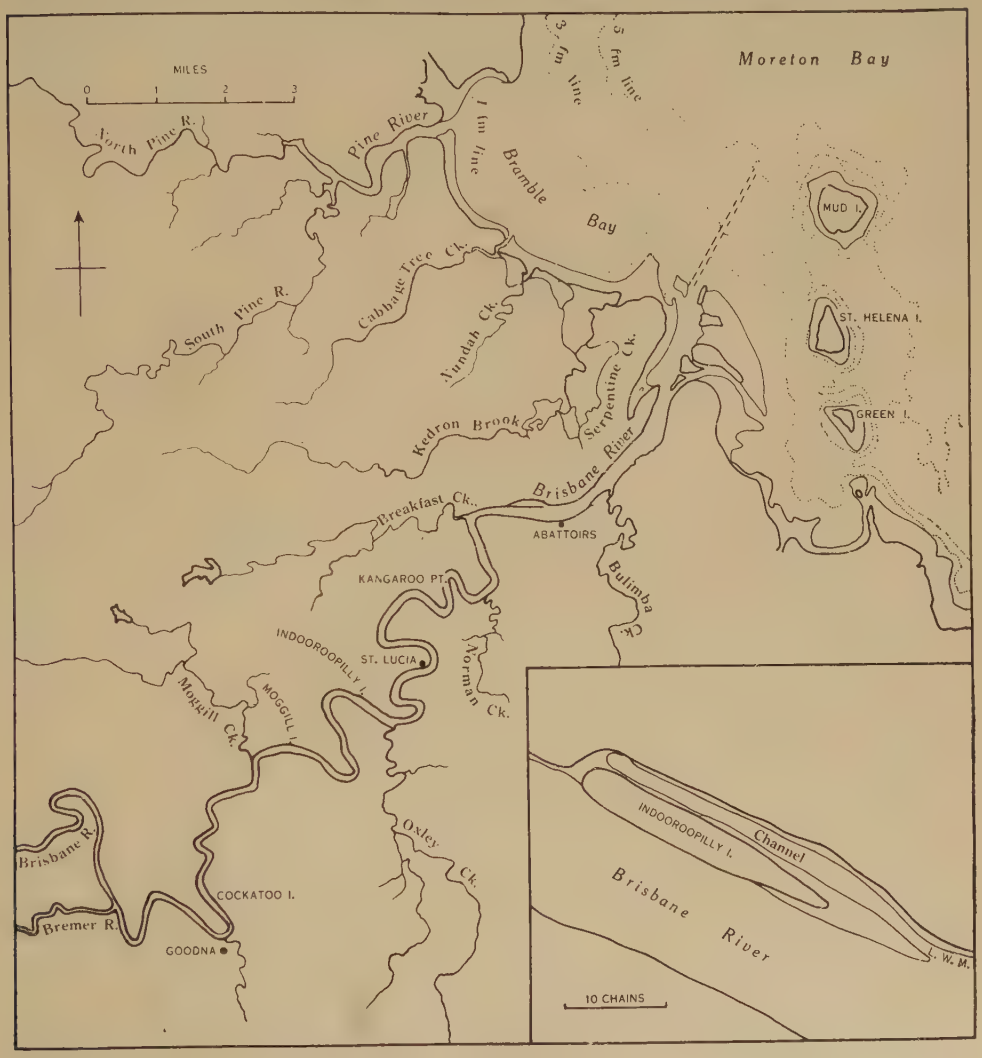

Fig. 1.—Map of the tidal portion of the Brisbane River. Inset: Indooroopilly I.

are provided by the inside channels of Indooroopilly, Moggill, and Cockatoo Is. (Fig. 1). These young stages occur in varying numbers throughout the year, except during floods which sweep most of the river fauna downstream. Larger juvenile prawns are abundant on more exposed shallow mud-banks during summer, but in winter and during floods numbers are greatly reduced.

(b) *Influence of Salinity and Temperature*

In the Brisbane River, tidal influence extends to about 60 miles upstream, tidal currents at some points reaching 2 kt. Freshwater stream discharge is usually at a minimum by late December, and rises to a maximum by late March following seasonal heavy rains (Queensland Irrigation and Water Supply Commission, *Annual Report for* 1953–54). Minor flooding may occur, and fresh water sometimes extends, on the surface at least, almost to the mouth. After March, the discharge decreases through the year. The effect of rainfall on salinity at Indooroopilly is shown in

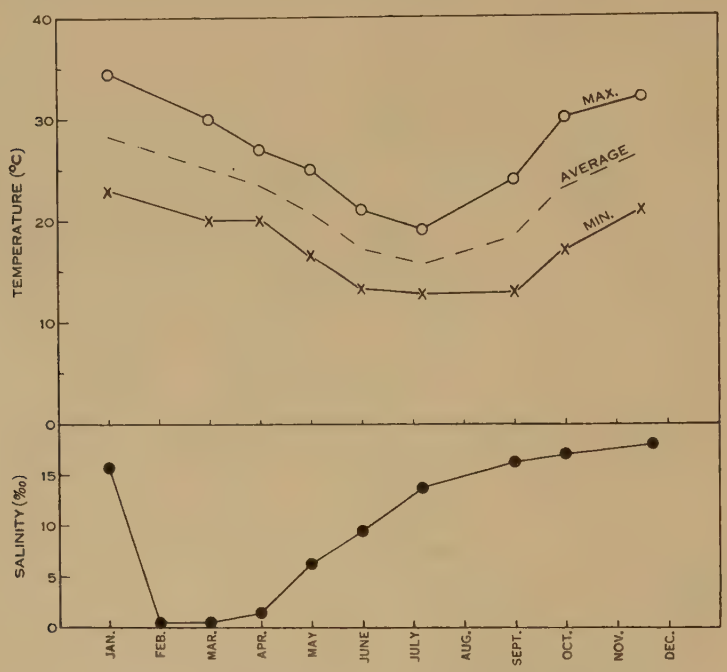

Fig. 2.—Salinity and temperature in the channel of Indooroopilly I., Brisbane River, during 1953.

Figure 2. Summer rainfall for 1952–53 was normal (Queensland Weather Bureau, unpublished data). The flood rains of February and March 1953 reduced the salinity to 0·11‰, which rose gradually to a maximum in December.

At the highest point sampled in the river (mouth of Bremer River, Fig. 1), a typically freshwater flora and fauna with abundant atyid shrimps were present. The salinity was 0·22‰ in June 1954, and four early postlarval *M. mastersii* were collected. At Goodna, where the salinity was 0·26‰, a short trawl yielded over 50 postlarvae (Fig. 7). Salinity, though not determined, was probably higher in January 1954 (Fig. 2), when prawns of almost adult size were collected (Fig. 7). Postlarval and small juvenile prawns were present at Indooroopilly, though in greatly reduced numbers, even during the flooding of March 1953. In Moreton Bay, where the largest sizes are obtained and where spawning occurs, salinities

of 30–35‰ are usual (C.S.I.R.O. Aust. 1952). All demersal stages of *M. mastersii*, especially postlarvae, are therefore extremely euryhaline.

Temperature (Fig. 2) was recorded with a maximum and minimum thermometer at about 2 ft below low water spring tides. Flooding had no obvious influence. The large difference between maximum and minimum temperatures was due to the relatively small volume of shallow water in the channel, almost completely enclosed at low water. For example, on December 16, 1953, with low water at midday, a surface temperature of 35°C was recorded in the channel, whereas that of the open river was 27·1°C. Prawn abundance was least when the average temperature fell to 16°C.

(c) *Indooroopilly Island* (Fig. 1, inset)

The channel on the north side of the island was found to harbour more postlarvae than any other part of the Brisbane River, and hence the habitat is of interest as a favourable "nursery ground". Both islands and adjacent banks are densely covered with tall mangroves, *Avicennia marina* (Forsch.), which shelter the channel from prevailing winds. The channel is about ⅓ mile long, 20–30 yd wide, and up to 3 ft deep at low water spring tides. The bottom is muddy gravel, partly covered by small algae and vegetable litter for most of the year.

During the winter months the green filamentous alga *Vaucheria* sp. predominated, reaching a maximum in early August, when it was very dense below low water mark, extending up to about mean tide level. The red algae *Gracilaria confervoides* (L.) Greville, *Caloglossa leprieurii* (Montagne) J. Agardh, and *Callithamnion* sp. were also present, with the diatom *Melosira* sp. epiphytic upon most. By the end of September *Vaucheria* sp. was uncommon, and tufts of *G. confervoides* were growing densely on the larger stones, with *Callithamnion* sp. interspersed or epiphytic upon it. By December the *Callithamnion* sp. had disappeared and *G. confervoides* was abundant. The latter continued to thrive throughout the summer, but the scouring action of minor flooding in February and March effectively cleared the channel of most algae. *G. confervoides* thereafter gradually recolonized the channel, but did not reach its former summer abundance, and *Vaucheria* sp. and other red algae reappeared once more in the cooler months.

The macrofauna of this region contained few species. During spring and early summer a large tanaid and an amphipod were common, but these disappeared by mid December. The sergestid *Acetes australis* Colefax, the crab *Halicarcinus australe* (Haswell), and a few juvenile palaemonid prawns (*Macrobrachium* spp.) appeared during September and became more abundant as summer approached. The palaemonids sometimes outnumbered penaeid prawns when the salinity was very low owing to minor flooding. Occasionally small portunid crabs (*Scylla serrata* Forskål) were caught during summer. In addition to *M. mastersii*, a few juveniles of *Penaeus esculentus* Haswell, *P. merguiensis* de Man, and *Metapenaeus macleayi* (Haswell) were taken during spring and summer.

Williams (1955*b*) found that the postlarval and juvenile stages of three species of Penaeinae favoured warm sheltered regions with plenty of cover. Indooroopilly I. channel provides such a habitat. The minimum temperature falls below 15°C

only during winter (Fig. 2). The alga *G. confervoides* and dead mangrove leaves provide abundant shelter. It is probable that some of the Crustacea listed above compete with *M. mastersii* in this ecological niche, especially *Acetes australis* and palaemonid prawns.

The "nursery grounds" of Moggill and Cockatoo Is. are topographically similar to that of Indooroopilly I., but do not support such an abundance of *G. confervoides* and other flora and fauna. The islands are further from the mouth of the river than Indooroopilly I., and salinities are lower. These factors are probably responsible for the smaller numbers of *M. mastersii* at Moggill and Cockatoo Is. (Fig. 7).

IV. Growth

Burkenroad (1951) discusses the difficulty in assessing the growth rate of decapod Crustacea by the three usual methods, and proposes instead that the rate of moulting, together with increase in size per moult, would give more reliable results. Difficulties in establishing this for a wild population of Penaeidae are almost insuperable. Lindner and Anderson (1956) used tagging methods successfully with prawns above 80 mm in length, but considerable effort and a well-organized fishery was necessary. Menzel (1955) and Racek (1957) marked prawns with vital stains, but the method has limited use. Length frequency distributions have been used to estimate penaeid growth by Weymouth, Lindner, and Anderson (1933), Anderson, King, and Lindner (1949), Gunter (1950), Fujinaga (1955), Ikematsu (1955), Kubo (1955), Menon (1955), and Williams (1955*a*); but Lindner and Anderson (1956) show that progressions of modes often give a spurious growth rate, and that caution is needed in evaluating results. Pearson (1939) and Menon (1952) measured growth rates in aquaria, and Johnson and Fielding (1956) hatched and reared *Penaeus setiferus* to maturity in large ponds, obtaining a growth rate comparable with that found by Williams (1955*a*).

Ideally a combination of most of the above methods should be used to find growth rates of Penaeidae. In the present investigation length frequency distributions and measurements of captive prawns have been used. Limited facilities prevented consideration of other methods.

(*a*) *Measurement*

Weymouth, Lindner, and Anderson (1933) state that the length from the tip of the rostrum to the tip of the telson is the most reliable measure of size for *Penaeus setiferus*, while Burkenroad (1934, 1951) contends that length does not reveal certain important increases in size, and that volume or weight should be used. Carapace length is the most convenient dimension, especially for preserved material. Hence it was necessary first to establish its reliability as a measure of size for *Metapenaeus mastersii*.

(i) *Linear Relationships*.—To determine whether carapace growth is isometric, the carapace length, overall length, and rostral length of 430 prawns were measured. Carapace measurements were grouped in 1·0 mm classes, and class averages are shown plotted against average overall lengths (Fig. 3). A straight line fitted by the method of least squares gave a good fit. The regression coefficient r (430 pairs

of measurements) was 0·994. The relationship to overall length was:

$$l = 1 \cdot 27 + 4 \cdot 67c,$$

where l is the overall length (mm), and c is the carapace length (mm).

The relationship of rostral length to carapace length (Fig. 4), was again linear, except for the portion OA. A straight line was fitted to AB as before. It seemed probable by inspection that the portion OA indicated allometric growth (Huxley 1932), and this was verified by fitting a curve to OA, the equation being

$$r = 0 \cdot 167c^{1 \cdot 73},$$

where r is the rostral length (mm), and c is the carapace length (mm). For the

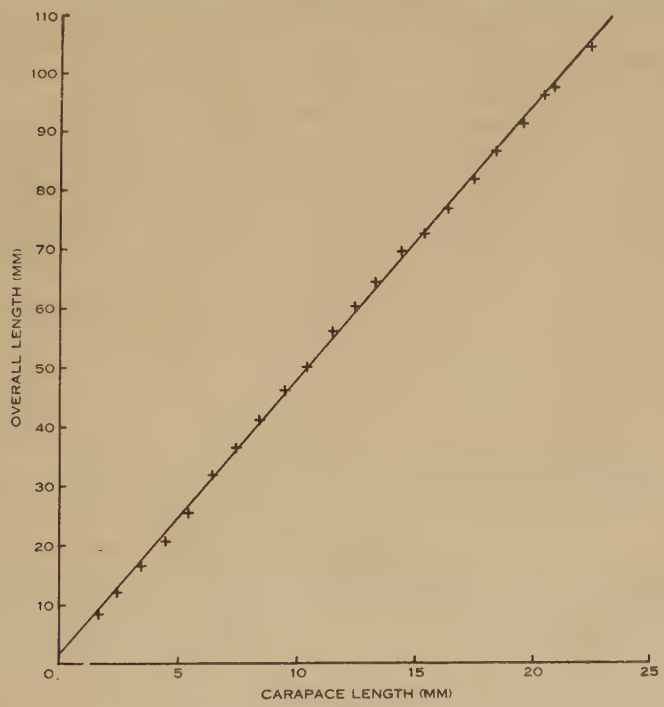

Fig. 3.—The relationship between carapace length and overall length (430 pairs of measurements).

portion OA, i.e. up to a carapace length of approximately 4·9 mm, rostral growth is allometric and this size marks the end of the postlarval stages (see Morris and Bennett 1952, p. 81, for description of postlarval stages).

There is no evidence for a decrease in relative length of the rostrum with increasing size in *M. mastersii* such as is stated by Burkenroad (1934) and Lindner and Anderson (1956) to occur in *Penaeus setiferus*, nor is there any for the greater variability of carapace compared with overall length (Weymouth, Lindner, and Anderson 1933). As with other Penaeinae (Kubo 1949), there is little evidence of marked allometric growth in the external features of juvenile *M. mastersii*, apart from secondary sexual structures (petasma, appendix masculina, and thelycum).

(ii) *Length-volume Relationship.*—To determine whether volume increased uniformly with length, 520 *M. mastersii* were measured for carapace length to 0·1 mm with 0·1 cm class intervals (length range 2–24 mm), and for volume by displacement (using a standard drying technique) to 0·005 ml for lengths below 10 mm, and to 0·05 ml above this size (Fig. 5). The parabola

$$V = 0{\cdot}33 - 1{\cdot}435c + 1{\cdot}93c^2,$$

where V is the volume (ml), and c is the carapace length (cm), gave a good fit.

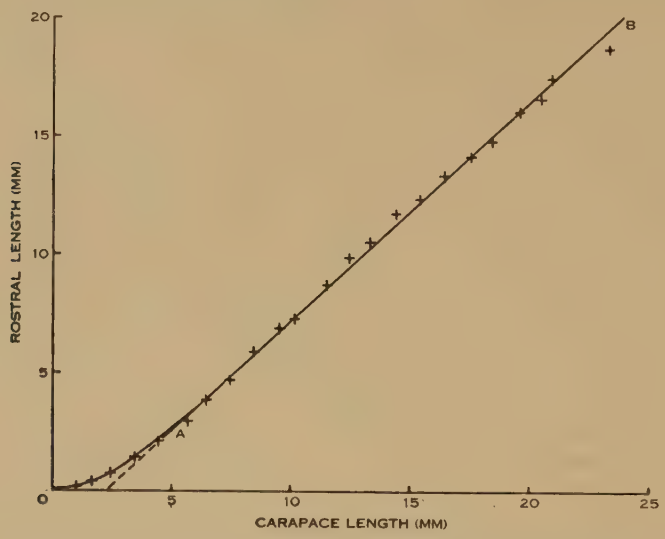

Fig. 4.—The relationship between carapace length and rostral length. *OA*, postlarval stages; *AB*, juvenile and adult stages.

If there were any increases in volume without corresponding increases in length these would be indicated by vertical deflections causing breaks in the continuity of the curve. There is no appreciable indication of this, and Burkenroad's (1934) assertion is not applicable to *M. mastersii.*

As the carapace does not grow allometrically in postlarval and juvenile *M. mastersii*, and the volume-length relationship is constant, carapace length was used as a measure of size. This is defined as the distance between the median posterior border of the carapace and a line joining the two orbital angles. Measurements were made to 0·1 mm with vernier callipers for prawns above 4 mm carapace length and to 0·075 mm with an eyepiece micrometer for smaller sizes.

(*b*) *Length Frequency Distribution*

(i) *Indooroopilly Populations.*—In the early stages of this work collections were restricted to the Indooroopilly nursery ground. This population was sampled at approximately monthly intervals from July 1952 to June 1954 (Fig. 6). Class intervals of 1 mm have been used throughout. Sexes were separated for length measurements above 3 mm from January 1953 onwards. Except for sizes above

14 mm in January 1954 from Hamilton and Bramble Bay, no difference in modes could be detected (see also Fig. 5). Accordingly sexes have been combined in the length frequency graphs.

During July and early August 1952 (Fig. 6) the distributions were similar, but with an increase in numbers in August. This large mode appeared to progress from 2 mm in August to 3 mm in September, 5 mm in October, 9–10 mm in November, and about 15 mm in December. A new mode at 4 mm in November

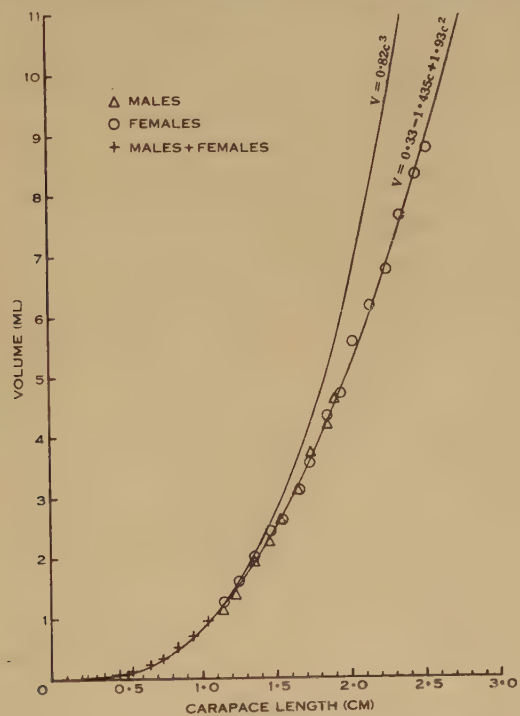

Fig. 5.—The relationship between carapace length and volume (520 pairs of measurements).

appeared to advance almost to 10 mm by December. Growth rate apparently increased as water temperature rose (Fig. 2). The maximum increase from November to December of 5–6 mm carapace length would give an increase in overall length of 24 to nearly 30 mm per month. However, the small mode at 3 mm in December only advanced to 6 mm in January. In the succeeding months when flooding occurred, there was a small displacement to the right and little could be deduced from the April distribution. By June the distribution was similar to that of the previous winter. In the spring of 1953 the principal mode advanced from 3 mm in September to only 7 mm in December. No progression could be detected in the January–March 1954 distributions, but the 2 mm mode of March appeared to progress to 6–7 mm by early June.

No consistent results can be obtained from the above progression of modes. Williams (1955*a*), Johnson and Fielding (1956), and Lindner and Anderson (1956)

obtained a summer growth of 30–50 mm per month for North American *Penaeus* spp. The apparent growth rate of *M. mastersii* of nearly 30 mm at the high temperatures (Fig. 2) of November–December 1952 is therefore possible, but subsequent progressions, especially those of spring and early summer of 1953, do not confirm this rate. An alternative explanation is that the same population was being sampled only to October 1952, where the skewed distribution was due to the influx of larger sizes, probably from upstream grounds. Williams (1955*a*, 1955*b*) and Lindner and Anderson (1956) have shown that growing Penaeidae tend to move downstream, and that a reverse movement occurs only during exceptional conditions. In

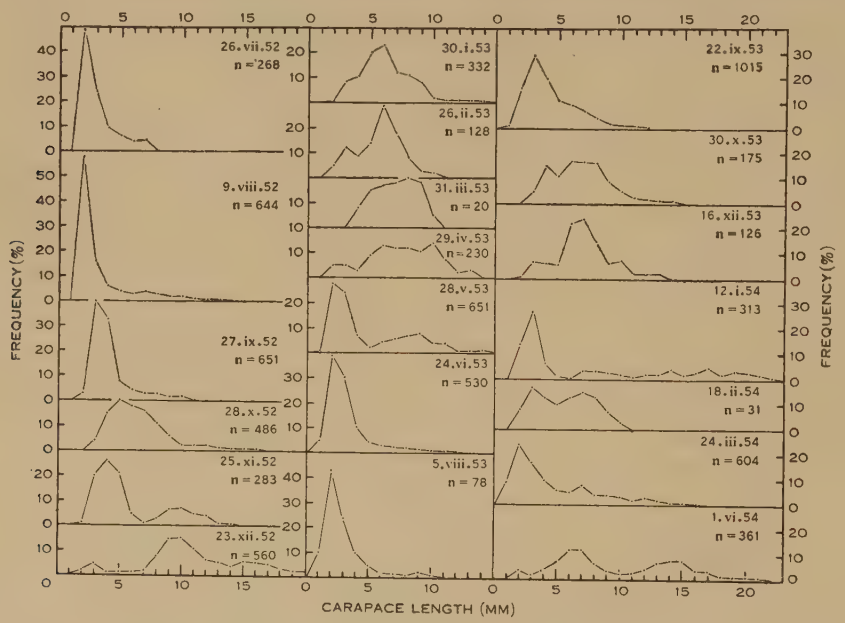

Fig. 6.—Length frequency distributions at Indooroopilly, July 1952 to June 1954.

November summer temperatures prevailed (Fig. 2), and most of the original Indooroopilly population had moved downstream. The left-hand mode represented the first arrival of postlarvae spawned in spring, and the right-hand mode a residual population or perhaps an entirely new group of larger prawns from upstream. These could have been augmented in December to give the principal mode, but could also be due to the greater proportion of larger sizes collected by the additional use of the seine net (mentioned in Section II). The mode on the right was undoubtedly due to this latter reason. These larger sizes could have been present earlier, but were missed with the scoop. The above explanation is applicable to the August–October 1953 distributions. The remainder show mainly that postlarval and small juvenile stages were predominant at Indooroopilly.

(ii) *Brisbane River Populations.*—As the Indooroopilly sampling indicated clearly that a more extensive series was required, various points in the Brisbane River were sampled from January to June 1954 as shown in Table 1. An additional sample was taken by otter trawl in Bramble Bay (see Fig. 1) in January.

For the January distributions (Fig. 7) it may be seen that at a given point in the river a certain size group predominated (neglecting Goodna, where the trawl was damaged). At Moggill and Indooroopilly there were large modes for 2–4 mm postlarvae, at St. Lucia a bimodal 6–12 mm group which had advanced slightly at Kangaroo Point, a 15–18 mm mode at Hamilton, and an 18 mm mode at Bramble Bay. It is possible to detect modes at 2–4 mm from St. Lucia upwards, at 8–12 mm from Kangaroo Point upwards, at 14–16 mm from Hamilton upwards, and at 20–22 mm from Indooroopilly downwards. These four modes may be interpreted as representing four distinct broods separated by roughly 5 mm, but the fact that there is a steady advancement of the principal mode from station to station downstream indicates that this is unlikely.

TABLE 1

LOCALITIES FROM WHICH SAMPLES WERE TAKEN, JANUARY–JUNE 1954

Locality	Miles from River Mouth	Type of Bottom	Months in which Collections were Made			
			Jan.	Feb.	Mar.	June
Brisbane Abattoirs (Hamilton)	4	Muddy shells	+	+		+
Kangaroo Pt.	11	Soft mud	+	+		+
St. Lucia	17	Soft mud	+	+	+	+
Indooroopilly I.	24	Muddy gravel	+	+	+	+
Moggill I.	32	Muddy gravel	+			+
Goodna (Cockatoo I.)	42	Muddy gravel	+*			+

* Trawl damaged, probable loss of postlarvae.

In February, following slight flooding, there was a marked depletion of numbers in the upper reaches, and the smaller sizes appeared much further downstream than previously, with a notable absence of the larger sizes above Hamilton. Except for the large sizes, the distributions in March at St. Lucia and Indooroopilly had returned to the January type, indicating a rapid recovery from the effects of flooding. There was no progression of the modes from January to March as would be expected if the former distributions showed four principal broods to be present.

In June there was a 2–3 mm group from Goodna to Indooroopilly, but distributions at both Moggill and Indooroopilly differed from the summer distribution. That of Moggill had a large mode at 11 mm and that of Indooroopilly modes at 6–7 mm and 14–15 mm. The Indooroopilly distribution is not unlike that of April 1953 (Fig. 6), and may indicate that the autumn type population was persisting later than in that year. The presence of only postlarval sizes at Goodna possibly presaged the beginning of the usual winter distribution at Indooroopilly.

From the foregoing it appears that in general a given region of the river may be associated with a certain size of prawn. As growth progresses the juvenile stages move slowly downstream. It is apparent that the growth rate of *M. mastersii* cannot

be measured by simple progression of the modes of length frequency distributions, for the greater part of the year at least.

Unless it has been established that the spawning period of a penaeid prawn is short, all estimates of growth obtained from frequency distributions should therefore be treated with caution, particularly when the sampling has been confined to one locality as in the work of Ikematsu (1955), Kubo (1955), and Menon (1955). Probably similar difficulties will arise in measuring the growth rates of any tropical and subtropical Crustacea having a reproductive phase long in relation to length of life.

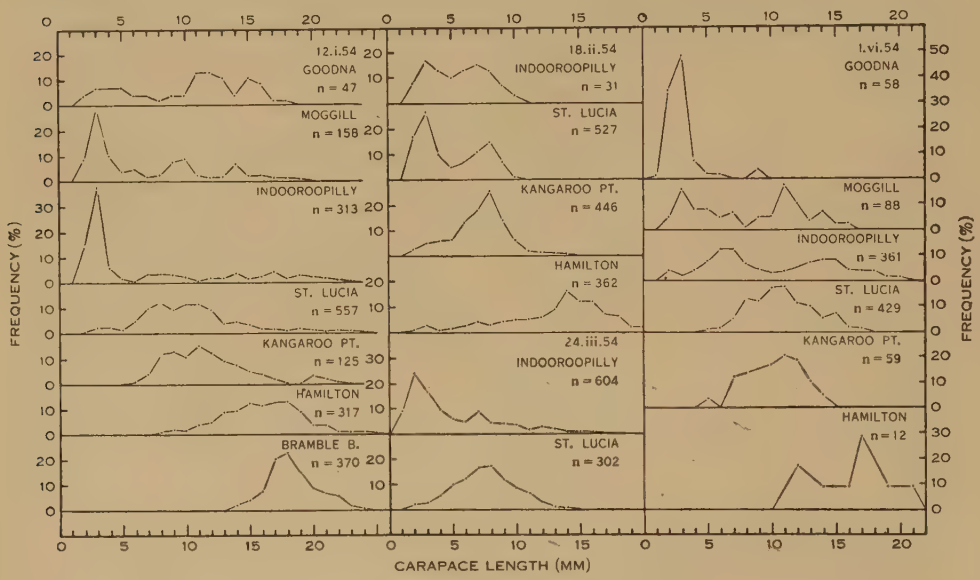

Fig. 7.—Length frequency distributions at various points in the Brisbane River (Table 1) and in Moreton Bay for January, February, March, and June 1954.

(c) *Growth Rate of Aquarium Specimens*

Pearson (1939) found that *Penaeus setiferus* below an overall length of 35 mm grew satisfactorily in aquaria of 1 gal capacity. *M. mastersii* thrives under aquarium conditions, and it was thought that the growth rate of the smaller sizes in aquaria would give some indication of the rate under natural conditions.

Seven prawns with carapace lengths of 1·9–7 mm (5·7–30·4 mm overall length), were collected at Indooroopilly (Table 2). Water of salinity 15·2‰ was used in the aquarium and fish-fry meal and dried shredded shrimp were used for food (about 0·5 ml of the mixture every second day) in conjunction with small amounts of finely chopped fresh fish (about 1 g every alternate day). Excess food was removed every second day. Aquarium temperatures (recorded with a maximum and minimum thermometer) ranged from 24 to 28°C. After 25 days the prawns were remeasured (Table 2). Apparently the larger prawns had moulted twice, but the smaller prawns could have moulted several times, as their exuviae are difficult to detect and disintegrate rapidly.

The smallest prawn was about the average size of the first postlarval stages found in estuarine waters and more than doubled its length in a month. The growth rate was slightly slower at a carapace length of 7 mm, but the average was 2·0 mm per month. At this rate therefore, it would take about 3½ months for the first postlarvae to reach a size of 9 mm. An increase in carapace length of 2 mm per month is an increase of about 10 mm in overall length. This is in accord with Pearson (1939) who obtained increases of about 10–20 mm per month for the larger *Penaeus setiferus* at 24–32°C, and Menon (1952) who measured increases of 7–14 mm per month for *Metapenaeus dobsoni* (temperature not stated).

TABLE 2

AQUARIUM GROWTH RATE OF M. MASTERSII

Data	Specimen No.						
	1	2	3	4	5	6	7
Carapace length (mm):							
At capture (10.i.55; surface temp. 28·5°C)	1·9	2·4	3·3	4·5	6·5	7·0	7·0
At 3.ii.55 (25 days at 24–28°C)	3·75	4·2	5·1	6·3	8·2	8·5	8·6
Increase in size (mm)	1·85	1·8	1·8	1·8	1·7	1·5	1·6
Increase in size (%)	97	75	55	40	26	21·5	23
Calculated increase in size for 30 days	2·2	2·15	2·15	2·15	2·0	1·8	1·9

Males of *M. mastersii* reach sexual maturity at a carapace length of 16 mm and females at 20 mm (see Section IV(*d*) below). From the aquarium growth rate, sexual maturity could be reached within 1 year. The aquarium growth rates also agree with the 2–3 mm progression of the modes of the September and October frequency distributions in 1952 and 1953 (Fig. 6). While recruitment from upstream grounds was possible, in these months spawning of the downstream adults had just begun, and the progressions may represent true growth. The absolute increase in length of the smaller sizes is likely to be greater than that of the larger sizes (Simpson and Roe 1939; Lindner and Anderson 1956). If *M. mastersii* reaches a carapace length of 9 mm in 3½ months, a length of 16 mm could be reached at an age of nearly 9 months and 20 mm at about 11 months, if an average rate of 1·5 mm per month were maintained. This assumes that growth is not influenced by temperature and that the growth rates of the sexes are not greatly different. The experiment was made at a temperature slightly below the maximum found under natural conditions (Fig. 2). Growth is probably faster at warmer temperatures, but may be greatly slowed, or even cease, at the lowest temperatures found (Lindner and Anderson 1956). The activity of *M. mastersii* was observed to be at a minimum in adults at 16°C, reaction even to strong stimuli being sluggish. Thus feeding and

hence growth may be suspended or much reduced for about 3–4 months of the year (see Section IV(*f*) below).

A prawn spawned in early November would overwinter as a 7 month pre-adult, and would be mature by October if a male and by December if a female. Those spawned late in the season would overwinter as postlarvae or early juveniles. If growth is more rapid during summer, it is possible that those spawned in late spring would be mature in autumn. The estimated time taken to reach sexual maturity

TABLE 3

LENGTHS OF IMMATURE AND MATURE MALE M. MASTERSII

Carapace Length Class (mm)	Immature		Mature	
	Mean Length of Class (mm)	Number of Measurements	Mean Length of Class (mm)	Number of Measurements
10–10·99	10·54	15		
11–11·99	11·47	15		
12–12·99	12·3	15		
13–13·99	13·57	15		
14–14·99	14·58	20		
15–15·99	15·34	23		
16–16·99	16·3	9	16·5	14
17–17·99			17·39	20
18–18·99			18·45	18
19–19·99			19·4	2
20–20·99			20·0	1

(12–15 months) is consistent with that found for other species by Weymouth, Lindner, and Anderson (1933), Pearson (1939), Hudinaga (1942), Menon (1952, 1955), Ikematsu (1955), Kubo (1955), Williams (1955*a*), and Lindner and Anderson (1956). The aquarium growth rate of *M. mastersii* is therefore taken as a reasonable indication of that under natural conditions.

(*d*) *Sexual Dimorphism*

That sexually mature males are smaller than mature females in Penaeinae is well established (Kubo 1949; Morris and Bennett 1952; Ikematsu 1955; Williams 1955*a*; and numerous authors listed by the foregoing). Morris and Bennett (1952) record that *M. mastersii* is sexually dimorphic.

The length-volume relationships of the sexes are the same (Fig. 5), and any sexual dimorphism must be only a size difference. To find the size at attainment of sexual maturity 164 males and 214 females were measured (Tables 3, 4). Male maturity was determined by the presence of a fully developed petasma (usually containing spermatophores), and female maturity by the presence of ovaries visible from the dorsal surface (King 1948). As overlap occurred in the 16–16·99 mm male class only (Table 3), with the majority mature, 16 mm was chosen as the average

size of attainment of sexual maturity. In females (Table 4) above 17 mm there was almost complete overlap of immature and mature groups. Below the 20–20·99 mm class the number of ripe females decreased sharply, while there were few immature females above the 22–22·99 mm class, and 20 mm was selected as an arbitrary maturity level. King (1948) states that ovaries of *Penaeus setiferus* become visible only during the last week of development, and "immature" females above 20 mm could therefore have been very nearly ripe.

TABLE 4

LENGTHS OF IMMATURE AND MATURE FEMALE M. MASTERSII

Carapace Class Length (mm)	Immature (ovaries not visible)		Mature (ovaries visible)	
	Mean Length of Class (mm)	Number of Measurements	Mean Length of Class (mm)	Number of Measurements
11–11·99	11·7	10		
12–12·99	12·2	10		
13–13·99	13·6	10		
14–14·99	14·32	10		
15–15·99	15·3	15		
16–16·99	16·5	15		
17–17·99	17·33	15	17·5	3
18–18·99	18·48	15	18·6	3
19–19·99	19·33	15	19·48	5
20–20·99	20·32	15	20·41*	14
21–21·99	21·4	14	21·55	10
22–22·99	22·34	9	22·64	5
23–23·99	23·6	6	23·33	7
24–24·99	24·34	5	24·15	2
25–25·99			25·17	3

* Arbitrary maturity.

(e) *Sex Ratios*

In Figure 8 the male/female ratios at Indooroopilly for 1953 and to June 1954 are shown. Flooding in February and March 1953 (Fig. 2) had a marked effect in reducing the ratio, and during winter also the relative numbers of males decreased. In 1954, heavy rains fell in February only, but the low ratio in January prior to the rains, was inexplicable. The June value was close to that of the previous year.

In Figure 9 the male/female ratios in the Brisbane River and Bramble Bay are plotted for January–June 1954. The higher values for Indooroopilly in January and December 1953 are also shown. Except in February 1954, males exceeded females 12–18 miles from the mouth, but above this region there was a marked reversal which persisted at 30 miles. In February 1954, following heavy rains, the relative numbers of males were markedly reduced at upstream stations.

These results indicate that approximately equal numbers of each sex are spawned, but that males are less tolerant of low salinities than females. The up-

stream male/female ratio increases with the higher salinities of summer, but the sharp drop of salinity following seasonal late summer rains results in the males moving well downstream. Female postlarvae may penetrate further upstream

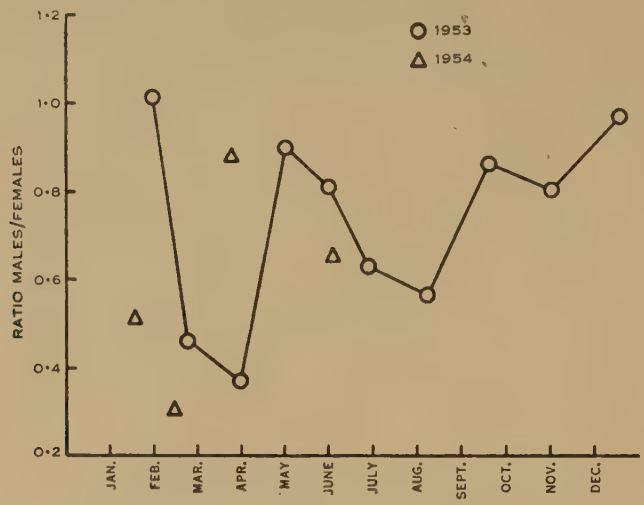

Fig. 8.—Male/female sex ratios at Indooroopilly, 1953 and to June 1954.

than males, but this is unlikely. Males probably reach sexual maturity earlier than females of the same brood (Ikematsu 1955; Lindner and Anderson 1956) and move downstream at a smaller size. Many of the males caught in January

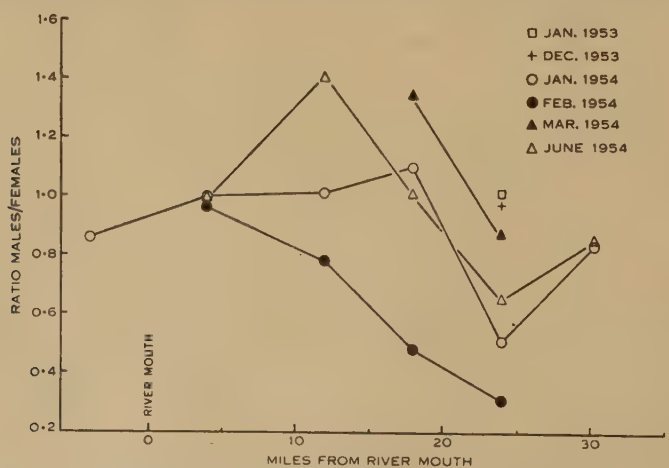

Fig. 9.—Male/female sex ratios for the Brisbane River, January and December 1953, and January–June 1954.

1954 4–18 miles from the mouth were mature, with spermatophores in the petasmas. A preponderance of females outside the river in Bramble Bay is shown in Figure 9, and indicates that males tend to be limited in their downstream migration. Females

with ripe ovaries were not taken in the lower reaches of the river, although many bore spermatophores. Thus there appears to be a predominantly male zone in the river, where impregnation of females occurs, the latter then continuing their downstream migration to the spawning grounds in Moreton Bay.

(*f*) *Growth Characteristics*

It would be expected that the length-volume data (Fig. 5) would follow a curve of the form

$$V = kl^3,$$

where V is the volume and l the length. Using logarithmic values, the best fit by the method of least squares for a curve of this type is

$$V = 0 \cdot 79c^{2 \cdot 76},$$

where V is the volume (ml), and c is the carapace length (cm), but this curve describes the data only approximately. The parabola

$$V = 0 \cdot 33 - 1 \cdot 435c + 1 \cdot 93c^2$$

gives a much closer fit, almost as close as that obtained from a cubic parabola (sums of residuals 0·2372 and 0·1985 respectively). However, the logarithms of values for immature prawns below 1·5 cm in carapace length give

$$V = 0 \cdot 82c^3.$$

This curve intersects the parabola when $c = 1 \cdot 1$ cm approximately (Fig. 5).

The departure of the higher values from the cubic length-volume relationship may be due to either:

(*a*) change in growth characteristics arising either directly or indirectly from the approach of sexual maturity. Most prawns above 1·0 cm in carapace length are moving downstream (Fig. 7) into higher salinities. Swimming activity has probably increased and food is different.

(*b*) the fact that all prawns measured were collected in January. Those below 1·0 cm would be 3–4 months old at the aquarium growth rate, or younger if growth were faster during summer, and in either case would have been spawned in spring or early summer. Those larger than 1·0 cm would have overwintered, and this part of the curve represents alteration of growth characteristics when feeding and growth are virtually at a standstill during winter. This occurs in *Penaeus setiferus* (Lindner and Anderson 1956), and explanation (*b*) is the more likely.

V. Behaviour

(*a*) *Burrowing Behaviour and Adaptations Thereto*

Although passing references have been made to the fact that penaeid prawns habitually bury themselves (Burkenroad 1934; Dakin 1938; Williams 1955*b*; Lindner and Anderson 1956; Young 1956), no detailed investigation of this seems to have been made.

When 11 adult *M. mastersii* were introduced in daylight into an aerated aquarium filled with sea-water at about 20°C, all sank to the bottom. Several merely remained there, quiescent, but the majority immediately began to bury themselves in the sand. The pleopods were spread out sideways and the substratum vigorously fanned backwards, the pereiopods meanwhile pushing it away in front. In this way a prawn could dig to its own depth in 5 sec, by which time all but the dorsal surface, eyes, antennules, and antennae was covered. The pereiopods then began to pull the body forward, the pleopods continued their movement, and the abdomen and posterior cephalothorax were rapidly drawn under the surface. Spasmodic movements continued until the dorsal surface of the abdomen of a prawn 80 mm

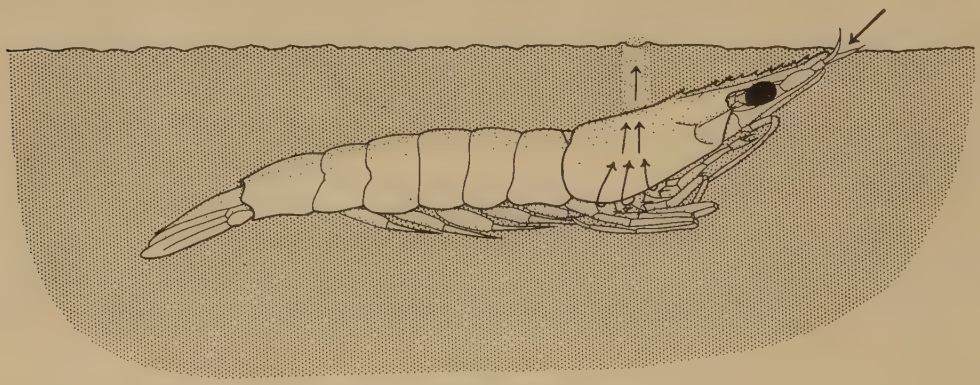

Fig. 10.—Semidiagrammatic representation of *M. mastersii* fully buried. Arrows indicate the direction of respiratory current.

long was covered to a depth of about 20 mm. The cephalothorax was inclined upwards with only the tips of the antennules, and sometimes the tip of the rostrum, protruding (Fig. 10). This behaviour was repeated on numerous occasions with various batches of prawns.

Further examination showed that the antennules and large antennal scales together formed a respiratory tube. The median surfaces of the antennules were closely apposed and the ventral surface formed a shallow arch anteriorly, and was flat posteriorly. The antennal scales met in an obtuse angle, and when applied to the antennules formed a wide canal. Dense interlocking fringing setae effectively sealed all edges. The opening at the base of the antennal scales was closed by the lamellar mandibular palps (Fig. 11). The canal then bifurcated, each branch leading to the anterodorsal region of the branchial cavity. Lamellar exites of the first maxilliped closed the anterior floor of the chamber, the scaphognathite lying immediately above it (Fig. 12).

By using carmine particles it was observed that water reached the branchial chamber via the antennal tube, and after passing over the gills escaped under the edge of the branchiostegite. When a prawn was buried, this escaping current of water was revealed by a small area of agitated particles, usually lighter than the surrounding substratum if the animal had been buried some time. Periodically the flow down the antennal tube was reversed in order to eject particles of sediment.

Water did not flow down the antennal tube when the prawn was swimming, the mandibular palps being raised to permit an almost direct flow to the branchial chamber. At all other times water passed down the antennal tube, unless, as noted above, accumulated particles began to block the flow.

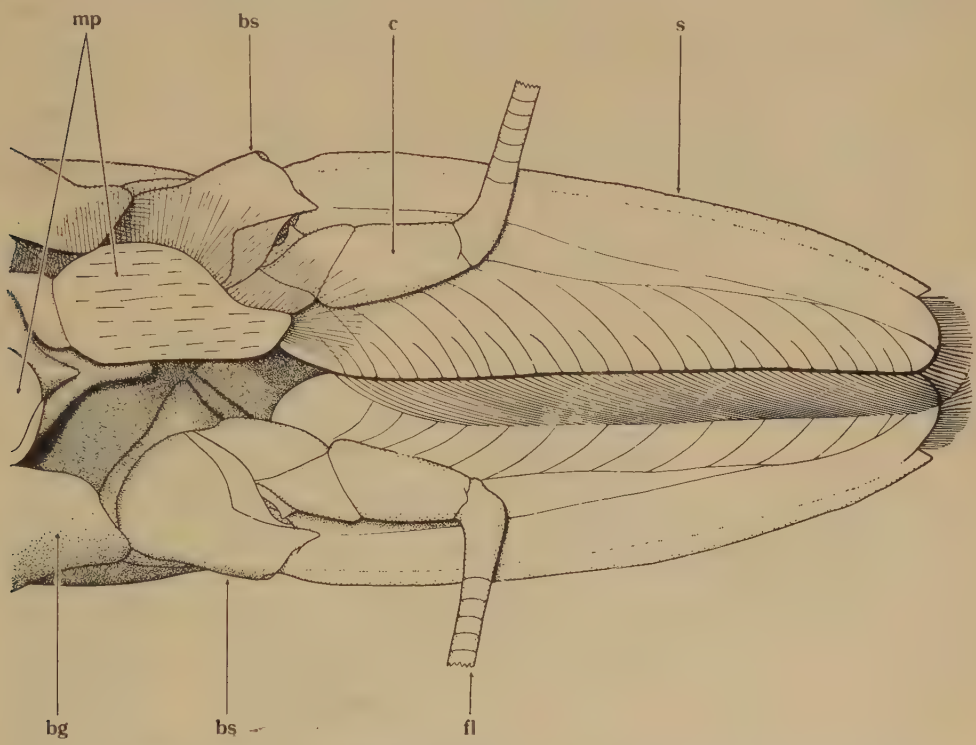

Fig. 11.—Ventral surface of the anterior region of *M. mastersii*, showing the floor of the respiratory canal formed by antennal scales (scaphocerites) and mandibular palps (the lower palp is reflected to show the canal; median and lower fringing setae omitted). *mp*, Mandibular palps; *bs*, basicerite or basal segment of antenna; *c*, carpocerite or fourth segment of antenna; *s*, scaphocerite; *fl*, antennal flagellum; *bg*, branchiostegite.

Burkenroad (1934) described a reversed respiratory flow in *Solenocera vioscai* Burkenroad (Penaeidae), associated with the habit of burrowing in soft silt. Structure of the antennae, antennules, and mandibular palps of Penaeinae, Eusicyoninae, and Solenocerinae (Kubo 1949) indicates that these subfamilies of the Penaeidae may all possess a similar respiratory current.

In *Macrobrachium novae-hollandiae* (de Man) (Palaemonidae) and *Cherax albidus* Clarke (Astacidae) the respiratory current was observed to pass under the edge of the branchiostegite and to escape forward at the base of the antennal scales. This is probably usual in most macrurous Decapoda, especially the Caridea, most of which have anterior appendages of a basically similar structure (Holthuis 1955). The reversed respiratory mechanism of the Penaeidae therefore appears unique among macrurous Decapoda.

(b) *Diurnal Behaviour*

At aquarium temperatures of 17–20°C adult *M. mastersii* did not emerge in daylight. At night all were invariably active, either swimming or searching for food. All would immediately bury themselves when an ordinary electric light was turned on.

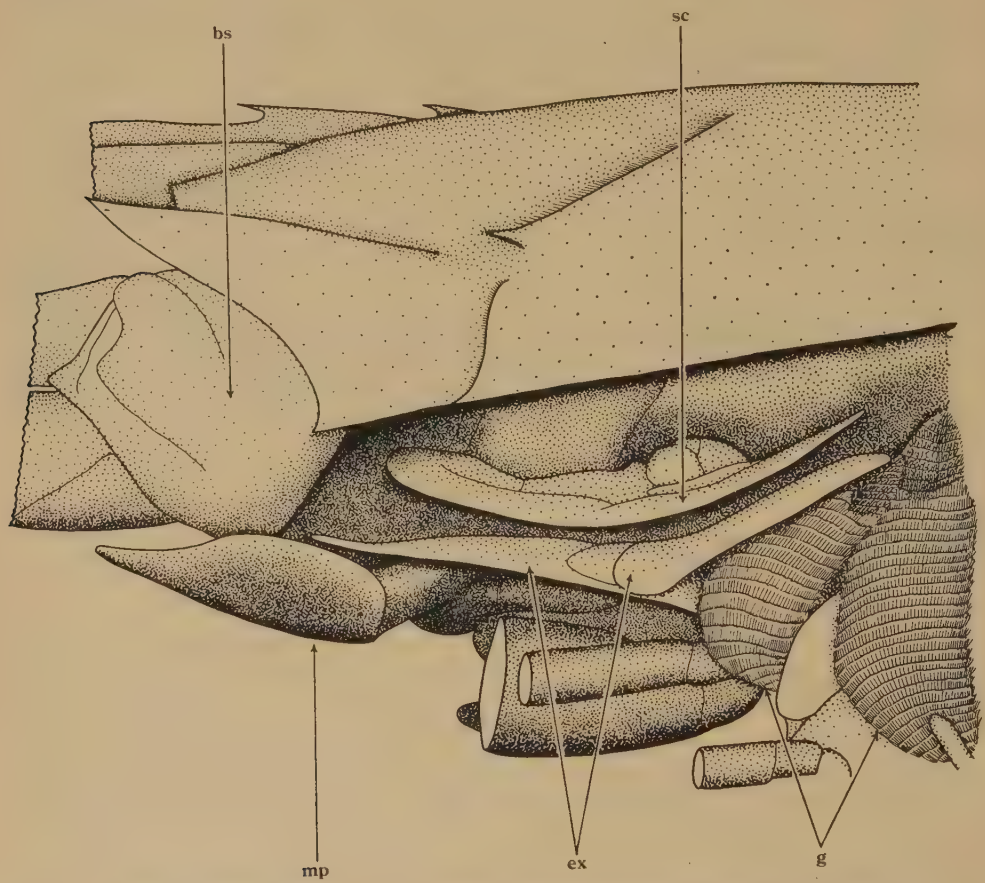

Fig. 12.—Lateral cephalic region of *M. mastersii* showing anterior branchial chamber. This is an extension of the canal shown in Figure 11, the ventral opening being closed by the exites of the first maxilliped. The scaphognathite is shown lying in the canal, which is directed towards the apex of the gills (branchiostegite removed; fringing setae omitted). *bs*, Basicerite; *sc*, scaphognathite; *g*, gills (arthrobranchs); *ex*, exites of first maxilliped; *mp*, mandibular palp.

A preliminary experiment indicated that this behaviour may be due to a diurnal rhythm as found in other decapods (Brown, Webb, and Bennett 1955). Two prawns were placed in a 2-gal aerated aquarium, which was kept in complete darkness except for quick inspections every 4 hr. Four prawns were maintained in an ordinary aquarium as controls. Temperature in both aquaria varied between 17 and 20°C. The prawns kept in the dark apparently remained buried during daylight for 7 days. On the 11th day there were signs of upset in the diurnal rhythm,

and by the 14th day the prawns emerged for irregular periods during daylight. Neither experimental animals nor controls responded to introduction of food during the day.

Brown *et al.* (1955) have shown that there may be an exogenous contribution to persistent diurnal rhythmicity under so-called constant conditions. The above results therefore need cautious evaluation. The rhythm does not appear to be as firmly established in juveniles below 9 mm in carapace length, which emerged when food was introduced during daylight, but buried themselves once more after about 1 hour's feeding activity.

VI. Conclusions

While many of the foregoing results indicate that further investigation is needed, some conclusions may be drawn regarding the bionomics of *M. mastersii* in the Brisbane River.

In summer, following impregnation in the lower reaches of the river, the females spawn at 3–5 fm in the semi-enclosed waters of Moreton Bay. The duration of planktonic life is probably of the order of 2 weeks (Pearson 1939, larvae of *Penaeus*, *Trachypenaeus*, and *Eusicyonia*). Postlarvae 1·5–2 mm in carapace length (5–7 mm overall) enter the river and penetrate upstream for 24–50 miles. When a sheltered shallow locality with abundant algal cover is reached, the postlarvae become demersal and remain there until the end of the postlarval period (carapace length about 5 mm, overall length 25 mm). The majority start to move downstream at this stage, but a residual group remains near the nursery grounds and almost reaches adult size there (Fig. 7). These are mostly females, which supports the evidence that males are less tolerant of low salinities and generally move downstream before females of the same size. Most males and females 8–10 mm in carapace length (overall 39–48 mm, 3–5 months old) occupy a region 10–18 miles from the mouth. At a carapace length of about 16 mm (7–9 months old), the prawns are within 10 miles of the river mouth. The males are now sexually mature, but a prawn of this size hatched in November would be close to winter, during which there is great reduction of feeding and general activity, the prawns burying themselves in sheltered localities. As the temperature rises in September, activity is resumed, and the first commercial catches of the season are obtained. Postlarvae reappear at Indooroopilly in November, presumably from spawnings in late October. Spawning extends from this month to May, as early postlarvae are present in the nursery grounds during this period, except during flooding. Postlarvae spawned in autumn overwinter in the nursery grounds, and enter commercial catches in the following March or April. The majority of prawns pass part of their lives under winter conditions.

When the salinity drops sharply after the heavy rains of February, the upper river population moves downstream. The larger sizes are most affected, especially when flood conditions prevail. Following the seasonal rains the commercial catches are greatly augmented. Thomson (unpublished data) found that the commercial abundance of eastern Australian prawns was related to seasonal rainfall. For *M. mastersii* this is due to the larger sizes normally present in the lower reaches of the river plus the residual large sizes from upstream grounds.

On many prawning grounds, especially upstream mud-banks, the greatest catches are usually obtained from dusk onwards as prawns emerge and resume feeding and migratory activities. A trawl would readily pass over a prawn buried as shown in Figure 10. At Hamilton, near the mouth, and in Moreton Bay, large catches are sometimes made during daylight for several consecutive days, followed by an apparent disappearance. This could be due to upset of the diurnal burying behaviour by the approach of sexual maturity.

It is of interest that no ripe females have been taken in the lower reaches of the Brisbane River, and it is unlikely that spawning normally takes place there. Morris and Bennett (1952) reported that *M. mastersii* may spawn in a closed coastal lake. While this is evidence of the adaptability of the species, in an open river system the life history is comparable with that of other Penaeinae.

M. mastersii is not caught in the deeper waters outside Moreton Bay. Prawns larger than 25 mm in carapace length are rare, and presumably most die after a full season of spawning (Lindner and Anderson 1956).

VII. Acknowledgments

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REPRODUCTION IN AUSTRALIAN PEARL OYSTERS (LAMELLIBRANCHIA)

I. PINCTADA ALBINA (LAMARCK): PRIMARY GONAD DEVELOPMENT

By D. J. Tranter*

[*Manuscript received June* 10, 1957]

Summary

The primary gonad of *Pinctada albina* consists of paired systems of confluent tubules ("follicles") opening to the exterior at laterally situated urogenital openings. There are no morphologically differentiated gonoducts; the gonads empty into a short ciliated genital vestibule through the primary gonad follicles. A duct from each kidney enters each vestibule just inside the urogenital papilla. There is no superficial difference between the gonads of male and female, except in colour: the testis is cream and the ovary yellow.

The follicles originate in the connective tissue behind the openings, and spread through the space between external epithelium and viscera, by invagination, branching, and ramification. As they do so they carry with them, attached to the follicle walls, the primary germ cells ("stem cells"). There are four main follicular systems on each side of the body, but as development proceeds they tend to coalesce. Soon the gonad loses its bilateral appearance and envelops the whole visceral mass.

The species becomes sexually mature in its first year, often within 4 or 5 months.

I. Introduction

This is the first of a series of papers on the breeding of pearl oysters. The genus *Pinctada* Röding is represented in Australian waters by the following species: *P. albina* (Lamarck), the "bastard pearl oyster"; *P. maxima* (Jameson), the "silverlip" or "goldlip"; *P. margaritifera* (Linnaeus), the "blacklip"; *P. fucata* (Gould), the "Ceylon pearl oyster"; *P. maculata* (Gould); and *P. chemnitzi* (Philippi). The last two species are comparatively rare in Australian waters, and in this study have not received as much attention as the other four (Plate 1, Fig. 1). Although economically unimportant, *P. albina* is much easier to obtain than the other species. Previously, virtually nothing of its biology had been recorded.

This paper describes the primary development of the gonad by which sexual maturity is reached; a second paper will deal with gametogenesis in greater detail; a third will discuss seasonal gonad development and change of sex. The more comprehensive studies on this species provide a basis for similar investigations on other pearl oysters, particularly the commercially important species *P. maxima*.

P. albina is known mainly from Australia, but its distribution is probably wider than this. It is essentially an intertidal or shallow water species and may at times form extensive beds, as at Crab I. (Torres Strait), Moreton Bay (south Qld.), and Scharapa Passage (Groote Eylandt) (Hynd 1955, Plate 13); it is an early settler

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in the succession of fouling organisms. However, the distribution extends into deeper waters (up to 30 fm), where specimens are frequently found attached to the valves of *P. maxima*.

II. Materials and Methods

Material was obtained from the above-mentioned beds, and from wharves, buoys, boat hulls, and other collectors in the Thursday I. area. The oysters were examined in the laboratory, where they were placed in large concrete aquaria supplied with running sea-water. Reserve stocks were kept in wire cages suspended from a bamboo raft anchored close to the laboratory. Once they attached, and provided they were not overcrowded, oysters grew well under such conditions.

For each specimen, records were made of gonad development and size. The extent of gonad development was referred to a scale of stages based on the area occupied by the gonad follicles relative to that in a ripe oyster. (The term "ripeness" is used here to indicate fullness of the gonad, and is distinguished from "maturity" by which is meant adulthood). Thus stage 0 designates an undeveloped gonad and stage 3 a ripe gonad; and stages 1 (Plate 2, Fig. 1) and 2 (Plate 2, Fig. 2) are intermediate.

Reference will be made to several metrical characters to define the size of specimens, and to directional axes. These features have been fully described by Hynd (1955). Briefly, the straight hinge line is dorsal (Plate 1, Fig. 2), and the open shell edge, directly opposite, is ventral. Anterior is indicated externally by the byssal notch and projecting byssus. The dorsoventral measurement (D.V.M.) is the longest axis in the dorsoventral direction. The "heel depth" is the thickness of the valve at the hinge line. "Live heel depth" is a little less than this, and being more convenient is used in preference. It is an indispensable aid in age determination.

III. Superficial Appearance of the Gonad

There is no visible trace of the gonad in juvenile oysters. However, urogenital papillae may be seen on either side of the body. They are situated inside the mantle and gills at a point immediately dorsal to the posterior retractor muscle as it passes through the visceral mass (Plate 2, Figs. 1, 2). Each papilla consists of a pair of lips guarding the external urogenital opening (Plate 3, Fig. 6).

The fully developed gonad is most conspicuous. It is not a discrete organ, but is wrapped around the "visceral mass", a composite organ consisting of stomach, associated digestive diverticula, and gut loop. The foot joins this mass anteriorly and the pericardium posteriorly (Fig. 1; Plate 2, Fig. 2) but these are free of gonad. In contrast to the condition in the immature oyster, the dark brown mass of digestive diverticula is completely obscured by the gonad "envelope" of the ripe oyster.

The male gonad is usually cream and the female yellow, the colours being derived from the gametes which show through the transparent external epithelium; otherwise there is no superficial difference between testis and ovary. Occasionally either gonad may be dark yellow in colour as the result of parasitic infestation. Plate 3, Figure 3, shows a parasitized gonad in section. Hynd (personal communication) believes the parasites to be *Bucephalus* larvae (Trematoda).

Studies on individual bivalve species suggest that there is in this group a common pattern of gonad structure, to which *P. albina* conforms (Herdman and Hornell 1904, *Pinctada fucata* (Gould); Roughley 1933, *Crassostrea commercialis* (Iredale & Roughley); Quayle 1943, *Paphia staminea* Conrad). *Mytilus edulis* L. (Field 1922) differs slightly, in that the gonad also occupies the lobes of the mantle. This is a common feature with mussels. In some of the Pectinidae (Gutsell 1930) there is a more fundamental difference: the gonad is divided into separate male and female areas which differ in colour.

IV. Histological Structure

Sections across the gonad reveal that it consists of a system of branched tubules, the number and size of which depend on the stage of gonad development (Plate 2, Fig. 1; Plate 3, Figs. 1, 2). They are referred to here as "follicles". The follicular system occupies the connective tissue space between outer wall and viscera.

The outer wall consists of a muscular layer in contact with an external epithelium. The vesicular connective tissue consists of a conjunctive web in which are situated the vesicular cells (Plate 3, Fig. 4). These are of varied size, shape, and appearance, but tend in general to be swollen, and about 7 μ in diameter. The nuclei may be round, oval, or slightly spindle-shaped, and vary from 2 to 4 μ in width; the chromatin is densely reticulate. The tissue is not developed in the gonad area to the same extent as in edible oysters (Roughley 1933; Bargeton 1942).

Each follicle consists of an outer sheath, the follicle wall, housing the developing germ cells. Except in the stage of germ cell development, there is no morphological difference between the various follicles of the one gonad. Early in development, they tend to be elongate in cross section; later they are oval or round. Around the walls of young follicles are large germ cells, the progenitors of the gametes. They are here termed "stem cells" (Plate 3, Fig. 5) and are probably derived directly from the primordial germ cell. Older follicles contain fewer stem cells but many gametes.

The follicles are confluent, and the main systems run together on each side of the body into a short vestibule which may be regarded as the main genital duct. The kidney duct enters this vestibule (Plate 3, Fig. 6) immediately before it opens to the exterior through the lips of the urogenital papilla previously described.

Any one section across the visceral mass will cut through a number of gonad follicles of varying ages; therefore should there be any difference between one follicle and another in the stage of germ cell development, this will be clearly shown. It is possible by this means to assess accurately the overall stage of gonad development. There is little difference in the level of germ cell development between one gonad area and another.

V. The Pattern of Development

The gonad arises from a pair of primordia situated immediately posterior to the urogenital papillae; they consist of thin layers of stem cells. As each layer spreads through the connective tissue, it becomes invested with a thin membrane to which these primary germ cells become attached. This may be regarded as an early follicle.

As it elongates, the follicle takes the form of a solid flattened tubule which branches and infiltrates through the connective tissue between external epithelium and viscera. As it does so, the primary germ cells (stem cells) are carried to the sites of future gonad development. The branching tubules may therefore be termed "primary follicles". Before long their walls move apart and a lumen is formed.

The primary follicles increase in length till they have spread longitudinally as far as possible. They then consolidate by giving off side-branches into the connective tissue; these are not morphologically distinct from the parent follicle except that the growing tip may be at an earlier stage of germ cell development. When a follicle

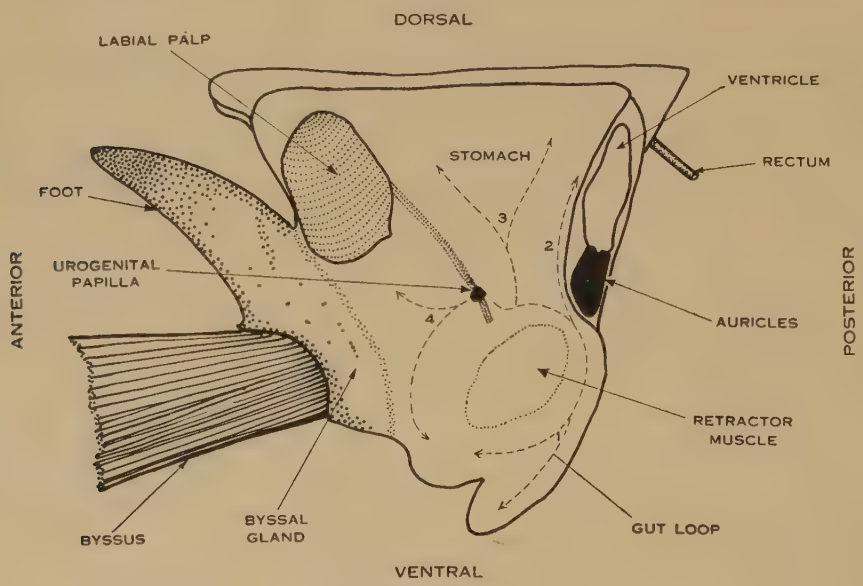

Fig. 1.—The spreading of the gonad follicles.

is established the stem cells cease to multiply and their derivatives begin to mature. As gametes form, the follicles increase in volume and soon become visible through the transparent outer wall; they show up as fine networks of white spreading out along well-defined paths from the genital pore regions on either side of the body (Fig. 1; Plate 2, Fig. 1).

One path leads around the dorsal edge of the retractor muscle, across the base of the gut loop, and spreads down its length; a second path branches off from this near the heart and extends up the posterior face of the stomach; a third, anterior to the heart, bifurcates early and spreads across the flat lateral face of the stomach; a fourth spreads anterodorsally immediately inside the gills, past the base of the foot and the byssal gland, toward the labial palps.

Lateral spreading fills in the interstitial spaces between adjacent follicular networks till they coalesce one with the other, and with those of the opposite side of the body. At the same time the follicles ramify vertically to form multilayers, and the gonad becomes considerably thicker. The primary gonad is now fully ripe.

The pattern of gonad development in this species closely resembles that described by Seurat (1904) for the Tuamotu blacklip, *P. margaritifera* var. *cumingi* (Reeve).

VI. Sexual Maturity

The early stage of primary gonad development (Plate 2, Fig. 1) is regarded as a period of adolescence. By the time the gonad has developed to stage 2 (Plate 2, Fig. 2) or stage 3, gametes are being produced in quantity within the follicles, and the oyster may be said to have reached sexual maturity. The mean size of oysters reaching this stage may be determined by referring to the associated records of gonad development and size. There is, however, one major difficulty: oysters with undeveloped gonads are not necessarily immature. It will be shown in later papers

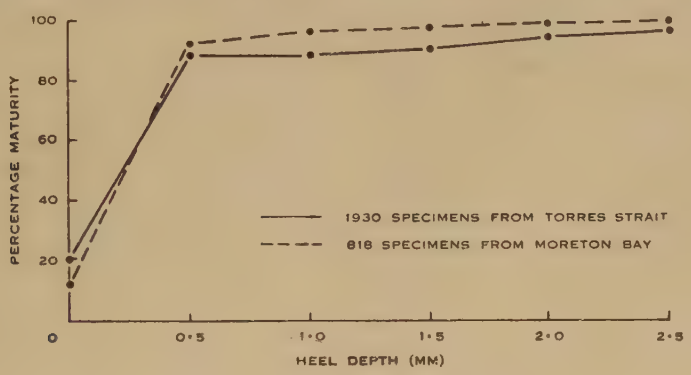

Fig. 2.—Onset of sexual maturity.

that in adult oysters a period of inactivity may occur after spawning, and small oysters at this stage may incorrectly be classified as immature. The frequency of inactive gonads, at least in the Torres Strait area, is at a minimum from November to April. Therefore, for purposes of determining size at first maturity, records taken outside this period are excluded.

If the percentage of mature specimens is plotted against heel depth, the onset and progress of maturity are indicated by a sudden increase in the percentage to a permanently high level. This has been done for populations from both Torres Strait and Moreton Bay. In both cases it is clear that maturity is reached at a heel depth of about 0·5 mm (Fig. 2).

The time taken for an oyster to reach this size has been determined by measuring specimens which have settled on cages, boat hulls, buoys, and other collectors submerged for a known period and whose maximum age is therefore known. Figure 3 shows the distribution of the collectors in the Thursday I. area. The largest oysters on collectors exposed for the same time are approximately of equivalent size no matter what time of the year the collector was laid (Table 1). As will be shown in a later paper, this is not surprising since spat settlement occurs throughout the year, and any one collector would be most unlikely not to receive representatives from all the minor and subsidiary spawnings, as well as a heavy spatfall from the major spawning. The

"conditioning period" before spat will settle on a new surface is less than a month, and the period of free-swimming larval existence has been given by Wada (1953) as 2–3 weeks. In general then, one may say that the age of the largest oysters from a collector is approximately equal to its period of exposure.

It is clear from Table 1 that the species may grow to a heel depth of 0·5 mm in about 4 months. Such growing conditions are of course better than average, owing to the cleaner, less crowded settling surface, and especially, in the case of light-buoys,

Fig. 3.—Map of the Thursday I. area showing the locality of collectors mentioned in Table 1.

to the shelter provided by the hollow cylinder stem. Under these conditions an oyster may grow to its maximum diameter within 12 months. Such vigorous growth, however, is not shown to the same extent in the heel depth dimension. There can be no doubt that, whatever the conditions, the species normally matures in its first year, and in all probability within the first 6 months.

It is an interesting point that most of the oysters examined in connexion with this work were male. This phenomenon will be discussed more fully in a later paper.

Pearson, Malpas, and Kerkham (1929) state that *P. fucata* also matures in its first year. *P. margaritifera* on the other hand (Talavera and Faustino 1931; Crossland 1957) is not sexually mature till the second year. Opinions are divided (Talavera and Faustino 1931; Wada 1953) as to whether *P. maxima* matures in its first year

or second. The ability of *P. albina* to mature in a matter of months is not unusual in bivalves; for example, Coe (1932*a*) found that *Ostrea lurida* Carpentier matures in 5–7 months, and Loosanoff (1937) that *Venus mercenaria* L. takes only 3–5 months.

TABLE 1

SIZE OF LARGEST SPECIMENS FROM COLLECTORS EXPOSED FOR KNOWN PERIODS

Collector	Date of Measurement	Time of Exposure (months)	Size of Largest Oysters	
			Heel Depth (mm)*	D.V.M.† (cm)
Sundry collectors	1954–1956	2	0	2·0
Possession I. collector	March 1956	4	0·5	4·2
Thursday I. cages	1954–1956	6	1·0	5·3
Possession I. collector	August 1956	9	1·5	7·0
Harrison Rock buoy	July 1956	12	2·0	8·0
Banda Rock buoy	October 1954	12	2·0	8·9
Marina Rock buoy	October 1953	12	2·5	10·0
Marina Rock buoy	October 1954	12	2·5	9·0

*To nearest ½ mm.

†Dorsoventral measurement.

VII. DISCUSSION

Various bivalve studies suggest that the gonad has its origin in the connective tissue between digestive diverticula and external epithelium (Coe 1932*b*, *Crassostrea virginica* (Gmelin); Loosanoff 1937, *Venus mercenaria*; Cole 1942, *Ostrea edulis* L.). However, in other species a more specific origin has been located, namely, near the genital pores (Field 1922, *Mytilus edulis* L.; Coe and Turner 1938, *Mya arenaria* L.). *P. albina* belongs to the latter group in this respect.

It is generally agreed that the bivalve gonad consists basically of a system of tubules. In some species these are differentiated into "ducts" and "follicles", the latter containing exclusively germ cells, the former with a well-developed ciliated epithelium opposite the "germinal epithelium" (Field 1922; Coe 1932*a*; Roughley 1933, *Crassostrea commercialis*; Cole 1942; Loosanoff 1942, *C. virginica*). The gonad products are apparently extruded through these ducts by ciliary action. We have already seen that there are no specially modified tubules in *P. albina*; the gonad products make their way to the vestibule via the primary genital follicles. There is, however, a tract of long cilia at the gonopore itself. Probably spawning in this species is effected more by pressure than by ciliary action.

As with most bivalve species, the prolific development of the gonad of *P. albina* relative to its other organs is most noticeable. It is probable that such accentuated reproductive potential is a direct response to the limitations of a sedentary existence.

VIII. Acknowledgments

This investigation was carried out at Thursday Island in the laboratory provided by the Queensland Government and maintained by the C.S.I.R.O. I should like to thank the Department of Harbours and Marine, Brisbane, for placing M.V. *Derwent* at our disposal, thus making it possible to sample the oyster population of Moreton Bay; and the Commonwealth Navigation and Lighthouse Service for allowing our officers to accompany the Lighthouse Vessel *Cape Leeuwin* on the annual buoy-servicing runs.

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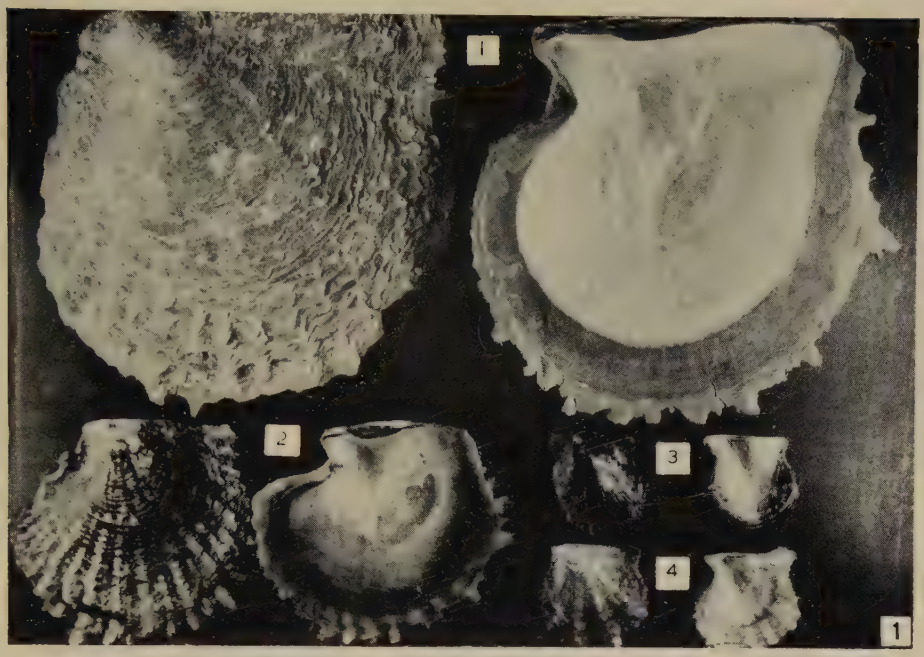
Explanation of Plates 1–3

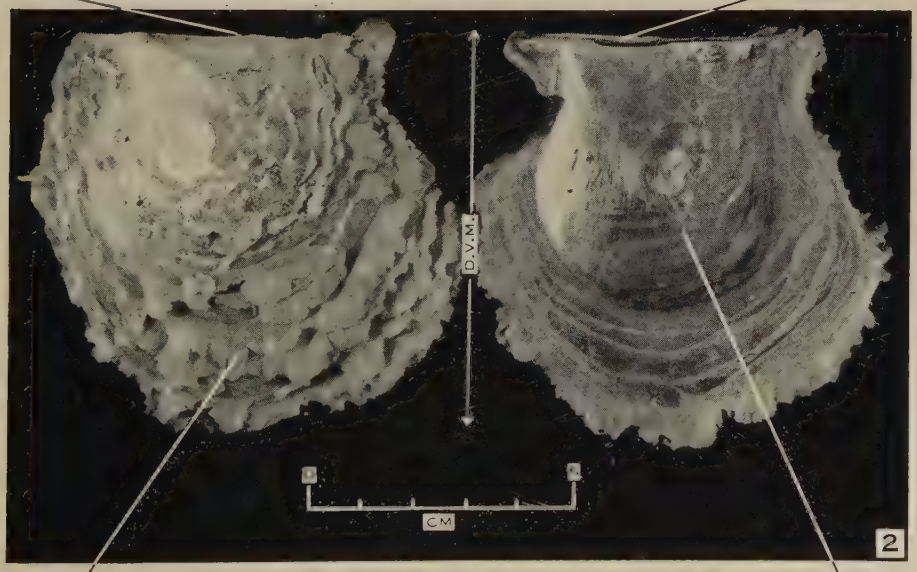
Plate 1

Fig. 1.—The common pearl oyster species of Australian waters: 1, *P. maxima*; 2, *P. margaritifera*; 3, *P. fucata*; 4, *P. albina*.

Fig. 2.—Orientation of the shell (*P. albina*).

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. I





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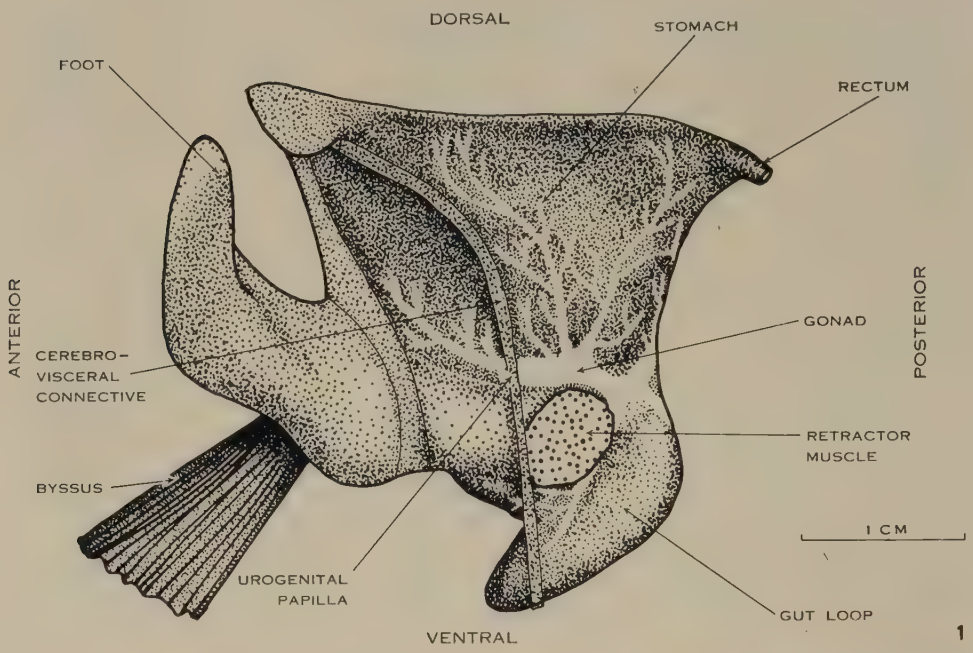

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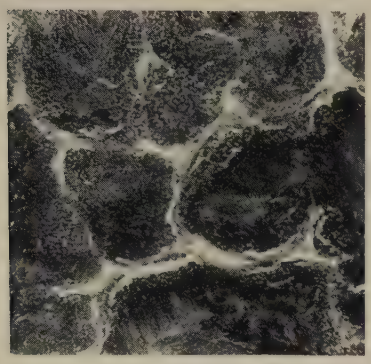

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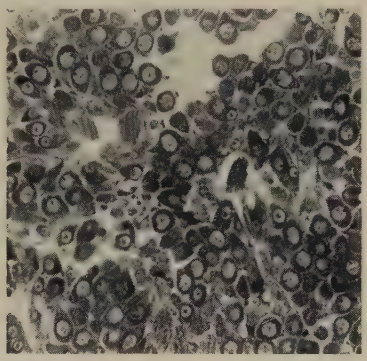
(1)



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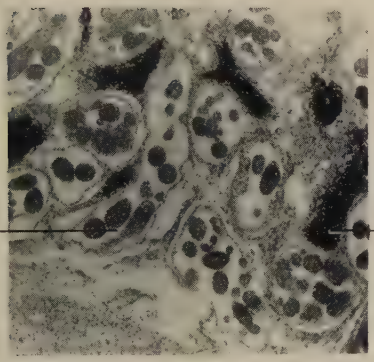

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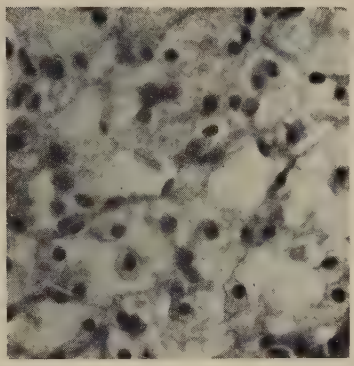
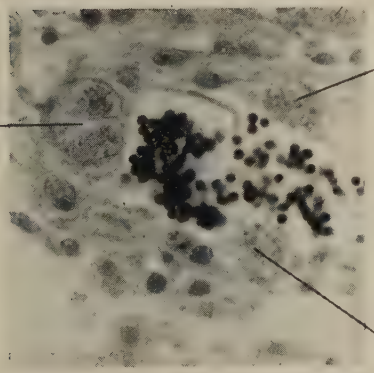


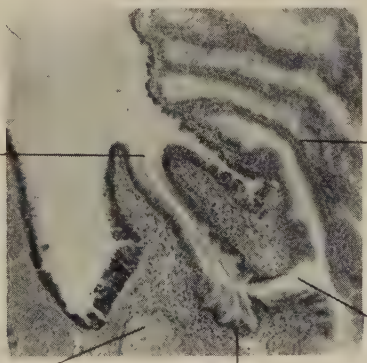
50 μ

(4)



15 μ

(5)



100 μ

(6)

PLATE 2

Fig. 1.—Gonad development, stage 1.

Fig. 2.—Gonad development, stage 2.

PLATE 3

Fig. 1.—Section across a ripe testis.

Fig. 2.—Section across a ripe ovary.

Fig. 3.—Section across a parasitized gonad (*p*, parasite; *mf*, male follicle).

Fig. 4.—The vesicular connective tissue of the gonad area.

Fig. 5.—Section across a young gonad follicle showing the stem cells (*s*).

Fig. 6.—The urogenital aperture showing the junction of kidney and genital ducts, and the urogenital papilla (*cvc*, cerebro-visceral connective; *gd*, gonoduct; *k*, kidney; *kd*, kidney duct; *ugp*, urogenital papilla).

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS (LAMELLIBRANCHIA)

II. PINCTADA ALBINA (LAMARCK): GAMETOGENESIS

By D. J. Tranter*

[*Manuscript received June* 10, 1957]

Summary

The developing germ cells of *Pinctada albina* are described and illustrated, and their origin is traced from the earliest (stem) cells of the gonad. The stem cell of the male gonad is not readily distinguishable from that of the female gonad; male and female germ cells appear, therefore, to have a common origin; obvious differentiation occurs just before they enter meiosis, the definitive oogonium being larger than the definitive spermatogonium. During early meiotic prophase, the chromosomes are more prominent in the female than in the male.

Non-germ cells associated with the gonad are described, and their function determined. The follicle wall is not a germinal epithelium, but a modified connective tissue. Phagocytic cells play an important role in resorbing unspent gametes.

The cycle of gonad activity—from earliest development through the stages of ripening, spawning, and recovery to subsequent redevelopment—is outlined. Whereas maturation proceeds to completion in the male, in the female, meiosis is arrested at prophase till spawning occurs. The spawning season is prolonged in both male and female, and spawning is often incomplete.

I. Introduction

Paper I of this series (Tranter 1958) described the primary development of the gonad in *Pinctada albina* (Lamarck). The present paper shows how the gametes are formed. The only work of this nature previously carried out on pearl oysters (Ojima and Maeki 1955) dealt with the Japanese species *P. martensi* (Dunker).

II. Materials and Methods

The material consisted of stained gonad sections belonging to two series:

(*a*) Samples drawn from the heterogeneous natural population, arbitrarily selected with respect to age and visible stage of gonad development. Total number examined, 200.

(*b*) Periodic samples throughout the year from a group of oysters of common origin, homogeneous with respect to age and size; thus the trend of the gametogenic cycle in an average individual may be inferred.

As a preliminary investigation, 80 oysters were taken from the hull of the M. V. *Pearline* on July 23, 1953, and were examined in batches of five at fortnightly intervals over the period August 1953 to May 1954. Subsequently a further group of 500 oysters, taken from the M. V. *Pelai* in February 1954, was examined in batches of 20 over the period March 1954 to February 1955. Most of the specimens were less

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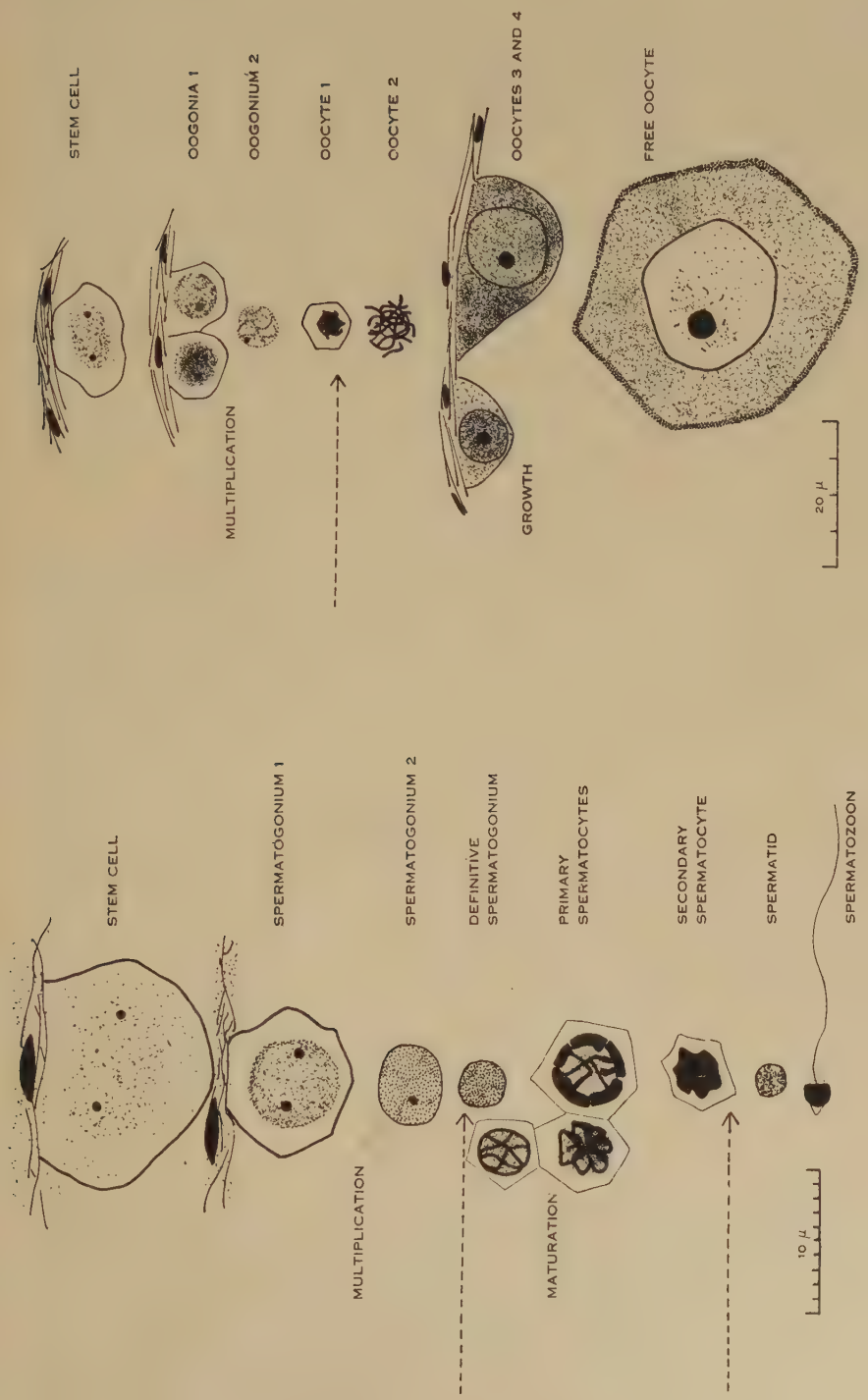

Fig. 1.—Relationship of the germ cells.

than 3 years old at examination. Until required, they were kept in cages suspended from a bamboo raft.

Before fixation, the sex of each specimen and its approximate stage of gonad development were determined from superficial examination and the microscopic study of gonad smears. It was established in an earlier paper (Tranter 1958) that a section across the visceral mass will cut through a number of gonad follicles of varying ages, giving a view of the condition of the whole gonad. Choice of the site for taking gonad samples is thus not critical; in the present study, gonad from the stomach area was commonly used, except in juvenile oysters, where tissues were taken from the genital aperture region thus ensuring that the first stages of gonad differentiation would not be missed. The most satisfactory fixative was Bouin's, which preserved nuclear detail excellently. Heidenhain's Susa was a better fixative for interstitial connective tissue. Final dehydration was with methyl benzoate, and the tissues were embedded *in vacuo* with paraffin, m.p. 56°C. Sections (7–10 μ) were stained with either Ehrlich's haematoxylin or crystal violet (Baker 1950), and counterstained with eosin.

III. Cell Types

(*a*) *Identification*

The identity of the various cell types in the gonad and the relation between them are by no means easy to establish. In studying the problem, particular attention was paid to relative distribution of the different cell types; to their size and density at all stages of gametogenesis; to gradations in nuclear size, amount of cytoplasm, and degree of basophilia; and finally to the distribution of dividing cells. Non-germ cells in the gonad could often be identified by reference to similar cell types in adjacent tissues.

(*b*) *Stem Cells*

Gametes of both sexes are derived from large, resting cells dispersed around the follicle wall. These have been termed "stem cells" (Tranter 1958). They are irregularly oval in section. Their long axis is parallel to the follicle wall and varies in length from 10 to 14 μ. The oval nucleus has a long axis of 7–10 μ. One or two small nucleoli (less than 1 μ in diameter) may be present, but are seldom very prominent. The outlines of the lightly staining diffusely reticulate nucleus are rather indistinct, and the substance of the nucleus seems to merge gradually into that of the lighter cytoplasm. Occasional mitotic figures are seen, particularly in primary gonad development. There is no consistent difference between the stem cells of testis (Fig. 1(*a*); Plate 1, Figs. 2, 4; Plate 2, Fig. 2; Plate 3, Fig. 3) and ovary (Fig. 1(*b*); Plate 4, Fig. 3; Plate 5, Fig. 3.)

(*c*) *Male Germ Cells*

(i) *Spermatogonia.*—Each stem cell gives rise by a series of divisions to a number of small (3–4 μ) round cells without visible cytoplasm. The densely reticulate nuclei possess no nucleoli, and the chromatin stains more heavily than does that of the stem cell. These cells, which have been termed "definitive spermatogonia" because they are the end products of spermatogonial mitoses, may be attached to the follicle wall, particularly in early development, but are more usually free. (Fig. 1(*a*); Plate 1, Figs. 2–4; Plate 2, Figs. 1, 3; Plate 3, Fig. 3.)

The series of spermatogonial stages between stem cell and definitive spermatogonium is characterized by a progressive decrease in cell, especially cytoplasmic, volume. At the same time the nucleus becomes more compact and basophilic. Nucleoli may still be seen in many cases. These cells have been termed "intermediate spermatogonia". Divisions of intermediate spermatogonia are rarely to be seen, probably because the process is very rapid. (Fig. 1(*a*); Plate 1, Figs. 2–4; Plate 2, Figs. 2, 4; Plate 3, Fig. 3.)

(ii) *Spermatocytes.*—The spermatocytes lie free in the follicle in a concentric band centripetal to the spermatogonia. Together with the latter, they appear at low magnifications as a lightly staining band surrounding a heavily staining core of spermatozoa.

Primary spermatocytes are derived directly from definitive spermatogonia by nuclear growth (3·5–5 μ). The nuclei vary in appearance as the chromosomes assume the various configurations of meiotic prophase. Within the spermatocyte layer in the follicle, there is no well-defined gradation in size from periphery to centre. There is a fine, faintly staining cell membrane and a clear cytoplasm, but these features are barely visible in the congested mass of nuclei. (Fig. 1(*a*); Plate 2, Figs. 1–3.)

Secondary spermatocytes are seen less commonly than primary spermatocytes. Apparently division is very rapid at this stage. They occur in groups, sometimes among the primary spermatocytes and sometimes further in toward the centre of the follicle. The nuclei are small (3 μ), irregular in outline, and very densely staining. The cytoplasm is clear, and bounded by a fine, distinct membrane (Fig. 1(*a*)).

(iii) *Spermatids.*—The spermatid nucleus is about 2 μ in diameter with densely reticulate chromatin. The staining is lighter than that of either sperm-head or spermatocyte, and resembles that of the spermatogonium. Spermatids lie in a layer or in groups, outside the central core of spermatozoa to which they give rise. (Fig. 1(*a*); Plate 2, Figs. 1, 3.)

(iv) *Spermatozoa.*—Spermatozoa are formed in the centre of the lumen. As they accumulate, the volume of less advanced germ cells decreases, until eventually the follicles are filled predominantly with spermatozoa. The sperm-head or nucleus stains a homogeneous, dense, dark colour with basic dyes. It is about 1·5 μ wide, and spade-shaped. The tail is very fine, about 30 μ long, and stains with eosin. The anteriorly placed acrosome may be distinguished at high magnifications (Fig. 1(*a*)) as a small, faintly staining, cone-shaped structure. (Fig. 1(*a*); Plate 2, Figs. 2–4; Plate 3, Figs. 1, 2.)

(*d*) *Female Germ Cells*

(i) *Oogonia.*—Oogonia are formed from stem cells by mitotic division. The "definitive oogonium" is larger than its counterpart in the male gonad, and the number of divisions from stem cell to definitive cell appears to be fewer. It is round in section (diameter 5·5 μ) and there is no observable cytoplasm. The nucleus is less homogeneous and stains less densely than the spermatogonium. There is often a small nucleolus (less than 1 μ diameter), peripherally or eccentrically placed. (Fig. 1(*b*); Plate 5, Fig. 3.)

Intermediate oogonial types are frequently observed. The most common of these is 8–9 μ in diameter, with a clear cytoplasm, and a nucleus (6–7 μ in diameter) similar

to that described above. The shape is determined by the pressure of adjoining cells, but tends toward roundness. In most respects they are similar to their counterparts in the male gonad. (Fig. 1(*b*); Plate 4, Figs. 1, 3, 4; Plate 5, Fig. 3.)

(ii) *Oocytes. Oocyte* 1 (*Leptotene*).—The earliest oocytes are characterized, strangely enough, by a mitotic arrangement, in which the chromosomes are tightly entwined in a densely staining clump (diameter 3–5 μ). This is situated slightly off centre in a clear nuclear cavity (diameter 5–8 μ) bounded by a fine irregular nuclear membrane. The chromosomes are in the leptotene stage of meiotic prophase, but have preserved the same arrangement as in the previous mitotic telophase (White 1950). There is no apparent cytoplasm. Growth and maturation of the primary oocyte commence at this point, giving rise to the various developmental stages described below. The oocyte 1 is homologous with Cleland's (1947) "definitive auxocyte" described in the Sydney rock oyster *Crassostrea commercialis* (Iredale & Roughley). (Fig. 1(*b*); Plate 4, Figs. 1, 2, 4; Plate 5, Fig. 4.)

Oocyte 2 (*Zygotene, Pachytene, and Early Diplotene*).—Following leptotene, the chromosomes become very distinct as they disentangle and spread through the nuclear cavity. The chromosomal area (7–8 μ) is greater than in the primary spermatocyte. In sections, groups of oocytes 2 contrast markedly with the lighter-staining mass of more advanced oocytes. There is no nucleolus. (Fig. 1(*b*); Plate 4, Figs. 2, 3.)

Oocyte 3.—The chromosomes lose their "fixability" (White 1950) toward the end of meiotic prophase. This feature may possibly be related to the reappearance and rapid growth of the nucleolus at this time. As the chromosomes enter what is considered to be a resting stage, there is a marked acceleration in the vegetative growth of the oocyte. The early growth stages have been designated "oocytes 3". Cytoplasm is laid down first of all, and the oocyte becomes connected to the follicle wall by a flat broad base of attachment; thus the cell becomes semi-oval in shape. The short axis measures 9–13 μ, and the spherical nucleus 7–9 μ. The cytoplasm stains less heavily than the nucleus. The nucleolus, when it reappears, is larger than that of the oogonium, and grows rapidly (1·5–2·5 μ). (Fig. 1(*b*); Plate 5, Fig. 3; Plate 6, Fig. 4.)

Oocyte 4.—The cytoplasm stains more heavily as yolk accumulates, and the nucleus less heavily as the chromatin disperses, until eventually the latter becomes the clearer of the two. These cells have been termed "oocytes 4". They increase in size, and, as the base of attachment constricts, become roughly spherical in shape. Later the stalk elongates and they become pear-shaped. The short axis varies from 13 to 35 μ and the nuclear diameter from 9 to 25 μ. The nucleolus continues to grow (2·5–4 μ), but the rate is slower than previously. (Fig. 1(*b*); Plate 4, Fig. 4; Plate 5, Figs. 1, 3, 4.)

Free Oocytes.—These are ripe oocytes which have become freed from the follicle wall into the lumen. Being more regular in outline than attached oocytes, they appear to be larger; however, it is doubtful whether there is any further growth after breaking away. The mean diameter varies from 35 to 40 μ. They are still immature ("primary oocytes"), and neither does the germinal vesicle break down nor do the chromosomes reappear, till spawning takes place. ("Immature" is used here strictly in the cytological sense.) (Fig. 1(*b*); Plate 5, Figs. 1, 2, 4.)

(e) *Non-germ Cells*

(i) *Cells of the Follicle Wall.*—The follicle wall is not a germinal epithelium in the true sense of the term. The constituent cells are long and attenuate and it is difficult to define their cytoplasmic limits; their nuclei are large and spindle-shaped, averaging 6 by 2 μ; both cell and nucleus are elongated along the wall at right angles to the longitudinal axis of the follicle. The appearance and function of these cells suggest that the follicle wall is a modified connective tissue. (Fig. 1; Plate 2, Fig. 4; Plate 4, Figs. 1, 4; Plate 5, Figs. 3, 4.)

(ii) *Intrafollicular Cells.*—It has been possible to distinguish within the follicle three different cell types which do not belong to the germ cell series. They apparently have a resorptive function, since they are found most commonly in spent follicles near residual matter. The three types have been designated A, B, and C and are described below:

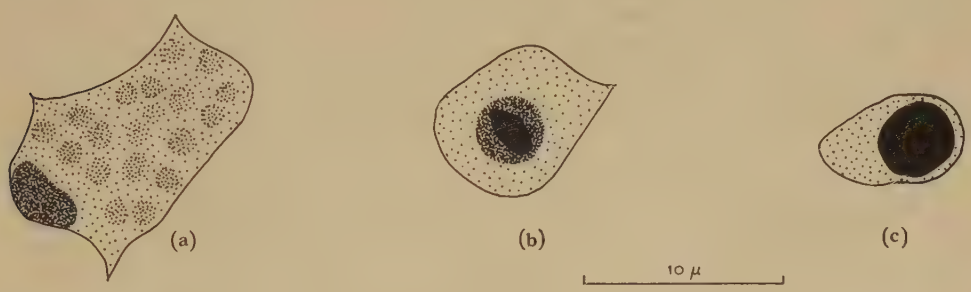

Fig. 2.—Intrafollicular non-germ cells: (*a*) cell type A; (*b*) cell type B; (*c*) cell type C.

Cell Type A.—The amoebocyte. This is the commonest of the three. It is amoeboid in appearance, with one or more pseudopodia. The size varies from 6 to 8 μ (mean diameter). The nucleus (2·5–3·5 μ) is oval and usually peripherally placed. It may be distinguished from the more reticulate nuclei of spermatogonia, with which it is most likely to be confused, by the dense homogeneous staining of its nucleus. Yellowish or greyish yellow granules may often be observed in the cytoplasm, and these impart to the cell its characteristic colour. The amoebocytes are usually aggregated together in a compressed mass around residual spawn. Their presence at such a time, and the visible degeneration of the residuum, leave no doubt that these cells are phagocytic in function. (Fig. 2(*a*); Plate 3, Figs. 3, 4; Plate 4, Figs. 3, 4.)

Cell Type B.—Whereas A has a granular cytoplasm, in B it is hyaline. The cell is, however, chiefly characterized by the presence of a densely staining chromatin core within the nucleus, occupying about half its volume. The cytoplasmic volume varies greatly. Sometimes it is restricted to a thin rim around the nucleus, while at other times there may be sufficient to engulf a whole degenerate egg. The nucleus is centrally placed. It is round or oval in shape, sometimes elongate, with a mean diameter of 3 μ. The nuclear core is variable in shape, often bar-like. Cells of this type are found most commonly in the ovary. A similar cell type may often be seen in the vesicular connective tissue outside the follicle. (Fig. 2(*b*); Plate 1, Figs. 2, 3; Plate 3, Fig. 4; Plate 4, Fig. 1; Plate 5, Figs. 2, 4; Plate 6, Fig. 2.)

Cell Type C.—Cells of this type are characterized by a large (3·5 μ), round, densely staining, pycnotic-like nucleus. The cytoplasmic volume varies greatly, and sometimes there is apparently none at all. The significance of this cell is not known. (Fig. 2(*c*).)

IV. Gametogenic Cycle

Depending on the environmental conditions, the speed at which gametogenesis proceeds varies greatly. It was shown in an earlier paper (Tranter 1958) that during summer the gonads of oyster spat may fully develop in less than 4 months. So too may the adult gonad. In general, however, gonad development takes 7–8 months, spawning 3–4 months, and recovery 2–3 months. These periods are by no means clear-cut: it is not unusual for gametogenesis to continue after the first spawning of the season; nor for the resorption of gonad material to commence before spawning is complete; nor for a new breeding cycle to be initiated during the later stages of recovery.

Gonad recovery is prolonged because spawning is seldom complete, and considerable gonad material must be resorbed to make way for the next gametogenic cycle. When the gonad develops more than once in the same season, as it sometimes does, overlapping of breeding cycles is even more marked. To determine the true state of the gonad, one must distinguish between the germ cells of the developing and the declining phases, and estimate the degree of development and regression respectively. It is impossible to do this except by microscopic examination of stained gonad sections.

Various aspects of the gametogenic cycle are discussed in the sections following.

(*a*) *The Follicle Wall*

The follicle wall reflects to some extent the broader trends of the gametogenic cycle. This is not surprising when one considers its intimate relationship with the young germ cells, and the fact that the whole cycle goes on within its bounds. Early in gonad development, the cells of the wall are broad and compact, but as the follicle fills they stretch considerably, and eventually come to be arranged in a single layer with the nuclei widely dispersed. The follicles spread and, the space which may be occupied being limited, they become closely apposed one to the other (Plate 3, Fig. 1).

As the gonad empties, the cells of the follicle wall slowly contract and adjacent follicles separate. As they do so they are collapsed by the pressure of the outer muscular layer and become oval, then elongate, in cross section (Plate 3, Fig. 4; Plate 4, Fig. 2). The follicles continue to contract and the vesicular connective tissue reorganizes between them. Before long they have completely recuperated and assume their original appearance.

(*b*) *Spermatogenesis*

Except for residual gametes, the only germ cells in early developing male follicles are stem cells and spermatogonia (Plate 1, Figs. 2–4). As development proceeds, the residual matter is gradually removed by phagocytic ingestion (Plate 1, Fig. 3; Plate 3, Figs. 3, 4). The phagocytes increase in number at the outset and disappear

gradually as the residuum is cleared away (Plate 1, Figs. 1, 2). Attached germ cells may also succumb to these resorptive processes. Division of phagocytes within the follicle has never been observed. There can be little doubt that they actively migrate through the follicle wall as the gonad empties, and leave in the same way when resorption is completed.

At an early stage where development has not gone beyond the formation of definitive spermatogonia, there is often a break in the continuity of the cycle (Plate 1, Fig. 2). The gonad may rest here before meiosis. When spermatogenesis proper begins, there is a rapid burst of mitotic division, producing spermatogonia in quantity (Plate 1, Fig. 4). As these grow into primary spermatocytes the chromosomes become clearly visible.

For a time the whole follicle is filled with spermatocytes and spermatogonia. Soon, however, spermatids and sperm materialize in the centre, and form a darkly staining core within the peripheral band of younger cells (Plate 2, Figs. 1, 2). It is now possible for spawning to take place, but usually this does not occur until the follicle is riper. Formation of spermatocytes keeps pace for a while with the production of sperm, and the volumes of each are roughly equal; but as the follicles approach their peak capacity the rate of spermatocyte formation slows down. This is evidenced by the retreat of the lighter-staining outer band toward the follicle wall, until practically the whole follicle is filled with sperm (Plate 2, Fig. 4).

The follicle may now be said to be ripe. The sperm tails are directed away from the follicle wall toward the centre, and show up as bright pink (eosinophilic) tracts against the blackness of the sperm-heads (Plate 3, Figs. 1, 2). The band of spermatocytes is greatly reduced. There are a few spermatogonia still attached to the follicle walls, and always an occasional stem cell.

Spawning takes place from the centre of the follicle, these cells being developmentally the oldest, and occurs at intervals over a period of several months. Some follicles are emptied more completely than others (Plate 3, Fig. 1). When spawning is protracted or incomplete, the follicles become filled with phagocytes (type A) which proceed to ingest the residual spermatozoa. There are occasional instances of non-spawning in individual oysters, and in such cases the entire sperm production is resorbed.

(*c*) *Oogenesis*

Early female development is in most respects very similar to that of the male. The author could not recognize female follicles with certainty unless oocytes were present. Younger oocytes are conspicuous by their meiotic configurations, and later oocytes by their size. The earliest recognizable stage in female development is characterized therefore by oocytes 1 and 2 (see Section III(*d*)), oogonia, and stem cells (Plate 4, Figs. 1, 3). The oogonia and early oocytes occur in self-contained groups around the follicle wall, and the stem cells here and there as in early male development.

The oocytes differ in size and appearance from spermatocytes of the same order, and their chromosomes are more conspicuous. They are a more or less permanent feature of the female cycle, but whereas they dominate the scene in the young follicle, in the older follicle they occur in the interstices between the stem attachments of older oocytes (Plate 5, Fig. 4). Their presence in the female follicle at all stages is

rather intriguing. It would seem that many young oocytes experience an arrestment of growth and of meiotic activity. This is probable for two reasons. Firstly, there is a limited attachment area. Whereas early in development, the stretching follicle wall is able to keep pace with oocyte growth, later in development the growth of young oocytes would be delayed till space were made available by the liberation of ripe oocytes into the lumen; this would result in an accumulation of young oocytes. Secondly, an arrestment of meiotic activity occurs in the auxocytes (= growing oocytes). Here the chromosomes, which up till then have been so conspicuous, lose their fixability and do not reappear till after spawning, when the germinal vesicle breaks down (marking the end of prophase).

As in the male, spawning of the female is usually intermittent and frequently incomplete. The spent follicles separate more rapidly than do those of the corresponding male phase, and during resorption the follicle wall is more closely applied to the residual mass (Plate 6, Figs. 1, 3). In the residual ovary, degenerate oocytes and pycnotic nuclei are frequently to be seen (Plate 6, Figs. 1–4), and there is a decrease in cell size and a breakdown of cell and nuclear membranes. Autolytic processes are probably partly responsible, but the resorption of unspent oocytes is due principally to phagocytosis. In the ovary, type B phagocytes are more frequently to be seen than type A which are so prevalent in the residual testis. The follicular lumina of residual follicles are divided up, by what appears to be a follicular "tissue", into a number of sacs each surrounding a residual oocyte (Plate 6, Fig. 1). This "tissue" actually consists of a number of phagocytic cells (Plate 6, Fig. 2). The oocytes, large as they are, have effectively been ingested, and are undergoing cytolysis. The only cells immune to phagocytic attack are the oogonia.

(*d*) *Characteristic Stages of Gametogenesis*

It is convenient for purposes of comparison to establish a series of arbitrary but easily recognizable stages in the cycle of gametogenesis. The following system is based on that used by Kesteven (1945) for the Sydney rock oyster, *Crassostrea commercialis*. Five stages of development and three of regression are recognized, these being determined in the main by the predominating cell type in the follicle. This system is used in a later paper to determine seasonal gonad development.

The stages of the male cycle are as follows:

Md_1 (male development, stage 1).—Predominantly spermatogonia and stem cells; few spermatocytes. (Plate 1, Figs. 2, 3.)

Md_2.—Predominantly spermatocytes and spermatogonia; few spermatids or sperm. (Plate 1, Fig. 4.)

Md_3.—Space occupied by spermatocytes now equalled by that of spermatozoa (and spermatids); few tailed sperm; few spermatogonia. (Plate 2, Figs. 1, 2.)

Md_4.—Predominantly spermatids and spermatozoa, many with tails; spermatocytes restricted to a band several cells thick around periphery of follicle. (Plate 2, Fig. 3.)

Md_5.—Almost exclusively spermatozoa, majority tailed; few spermatocytes; occasional follicles partly emptied. (Plate 2, Fig. 4.)

Mr_1 (male regression, stage 1).—As above except that many follicles are partly or completely empty; in others, the mass of sperm has lost its continuity with the cells around the follicle wall; occasional phagocytes within the follicles (Plate 3, Figs. 1, 2).

Mr_2.—Follicles still further emptied and phagocytes at a maximum; residual sperm much reduced but still noticeable, and tending to aggregate in the centre of the lumen.

Mr_3.—Follicles completely empty except for phagocytes and an occasional group of residual sperm (Plate 3, Fig. 3).

The stages of the female cycle are as follows:

Fd_1.—Oogonia and young oocytes numerous; latest stage, oocyte 2 (chromosomes conspicuous). (Plate 4, Figs. 1–3.)

Fd_2.—Largest oocytes have nuclei darker than cytoplasm, chromosomes indistinct (oocytes 3); these as numerous as oocytes 1 and 2; oogonia still abundant.

Fd_3.—Nuclei of oocytes frequently lighter than cytoplasm, much larger than previously, but still attached to the follicle wall (oocytes 4). (Plate 4, Fig. 4.)

Fd_4.—Free oocytes and attached oocytes equally numerous (Plate 5, Fig. 1).

Fd_5.—Practically all oocytes free and large; follicles crammed full; young oocytes few by comparison. (Plate 5, Fig. 2.)

Fr_1.—As above, but now indications of cytolysis and pycnosis; many follicles partly or completely empty; a few phagocytes.

Fr_2.—Follicles still further emptied; many degenerate oocytes; phagocytes common. (Plate 6, Figs. 1–3.)

Fr_3.—Only a few oocytes left in entire gonad (one or two may be seen in each section); resorptive "tissue" still present; usually gonad beginning to redevelop. (Plate 6, Fig. 4.)

In addition to the above, a further stage is introduced to define an undifferentiated, inactive condition of the gonad which often occurs between gonad regression and redevelopment. The stage is designated i (= inactive)—follicles either empty or contain only stem cells; phagocytes frequently present (Plate 1, Fig. 1).

In practice, the phases of regression are often overlapped to some extent by those of the new developmental era, and stages commonly found are Md_1/Mr_3 (Plate 1, Fig. 3), Fd_2/Fr_2, etc., as well as the "purer" conditions Md_1, Md_2, Fd_1, Fd_2, etc., which usually occur after a resting period. Occasionally the gonad redevelops as the opposite sex and must be classified as, say, Md_2/Fr_4. Such cases are fully discussed in a later paper.

One often finds that several follicles are not at the same level of development or regression; they are slightly out of step with each other (Plate 5, Fig. 3). This is often due to late outbranching and eversion from the main follicles. In such cases a number of follicles must be examined.

V. Discussion

The term "germinal epithelium" is often used rather loosely. Strictly speaking, such an epithelium is one whose constituent cells become differentiated into germ cells; it follows, then, that in such cases the epithelium is essentially a part of the gonad, and derived from the same primordial cell. There is little resemblance in *P. albina* between the follicle wall cells and the earliest recognizable germ cells (stem cells); nor are there any gradations between the two. The stem cells arise, not from the follicle walls but from a restricted region near the genital pores (Tranter 1958), and the follicles are merely the means by which they are spread in primary development throughout the potential gonad area. There is, however, a morphological resemblance between the cells of the follicle wall and those of the vesicular connective tissue; in addition, they have the common ability to stretch or contract as occasion demands. It seems reasonable to conclude, then, that the follicle wall of *P. albina* is not a germinal epithelium, but a connective tissue modified by the gonad to serve its various needs—such as nourishing the young germ cells, housing the gametes, etc.

Recognition of young germ cells in bivalves is seldom easy, particularly in those species where both sexual phases may develop in the same gonad follicle. In the literature, descriptions of oogonia are few, but most workers agree that the "sperm mother cell", or spermatogonium, is comparatively large, with a large vesicular nucleus and one or two nucleoli. Reference has often been made to "indifferent germ cells" (Coe 1931, 1943; Roughley 1933; Loosanoff 1937, 1942; Coe and Turner 1938; Quayle 1943) which differentiate into either spermatogonia or oogonia. Cole (1942) has found in *Ostrea edulis* L., however, that spermatogonia may be distinguished from oogonia at the earliest developmental stage; he has found that the oogonia have a larger, more vesicular nucleus, and a more prominent nucleolus. As far as *P. albina* is concerned, one must agree with the former workers, for the "indifferent germ cell" and the stem cell are obviously homologous. Although the definitive male and female gonia of *P. albina* may be distinguished from each other, it is not yet possible to distinguish between their predecessors. Of the bivalves so far investigated, the species whose germ cells bear most resemblance to those of *P. albina* are *Paphia staminea* Conrad (Quayle 1943), *Crassostrea commercialis* (Roughley 1933; Cleland 1947), and of course *Pinctada martensi* (Ojima and Maeki 1955).

As in the case of *P. maxima* (Wada 1953), the oocytes of *P. albina* do not mature within the gonad follicles nor, when they are extracted from the ovary, do they do so in sea-water or in the presence of ripe spermatozoa. In each case the germinal vesicle remains intact, showing that the meiotic cycle is still quiescent. This is a most unusual feature, and makes the artificial fertilization of pearl oyster eggs extremely difficult. Nuclear (germinal vesicle) breakdown occurs during spawning. A similar but unrelated effect is created by degenerate oocytes undergoing pycnosis. (Plate 6, Fig. 1.)

Perhaps one of the most striking features about the gametogenic cycle of this species is the preponderance of phagocytic cells within the follicles, after spawning and during early development. Evidence as to the resorptive function of these cells in *P. albina* is often indirect, but none the less convincing. In many cases, however,

degenerate germ cells may actually be seen inside the phagocytes, and there can be no doubt that they have been ingested; further, the degeneracy of such germ cells can be traced through to the stage where they are barely recognizable.

The resorption, in bivalves, of residual germ cells by phagocytosis has already been suggested or described by Roughley (1933), Loosanoff (1937, 1942), Coe (1943), Bargeton (1943), and Cleland (1947). Roughley thought that resorption in *Crassostrea commercialis* was carried out by an intrafollicular tissue allied to the vesicular connective tissue outside the follicle. Bargeton noted the presence of a similar intrafollicular resorptive "tissue" in *C. angulata* (Lamarck), but distinguished it from the vesicular connective tissue on histochemical grounds. Korringa (1952), reviewing the conclusions of these workers, suggested that the "tissue" is probably no more than a crowded accumulation of phagocytes. The present author has examined preparations of *C. commercialis* and has found, like Roughley, that it is not unlike a condensed vesicular connective tissue; a closer examination, however, confirms Korringa's supposition that it consists entirely of phagocytes; as in the case of *P. albina* several phagocytic cells may combine to surround and resorb large particles of residual matter (such as oocytes).

Takatsuki (1934) studied extensively the amoebocytes of *O. edulis* and found them to be distributed throughout the body, particularly around the gut. He recognized two main types: (1) granular (leucocytes); (2) hyaline (lymphocytes). The cell types A and B of *P. albina* (Fig. 2(*a*), (*b*)) are probably homologous with these. Cell type C (Fig. 2(*c*)) may be homologous with the "degenerating leucocyte" of Kollmann (1908) which also has a dense, deeply staining nuclear mass.

The essential role played by bivalve phagocytes in digestion and excretion is well known. It is the author's opinion, however, that the importance of their role in the reproductive cycle is not generally realized.

Most of the bivalves so far investigated inhabit temperate seas, and it is generally agreed that there is a dormant period in the gametogenic cycle during the colder months. Cole (1942) has found that *O. edulis* may winter at almost any stage of maturity. Loosanoff (1937) states that in *Venus mercenaria* the dormant period does not always coincide with winter; there is often active gametogenesis at this time, and the gonad becomes dormant later. The gametogenic cycle of *P. albina* tends toward winter dormancy, but this is by no means a universal feature.

The work of Ojima and Maeki (1955), being the only published account dealing with gametogenesis in pearl oysters (*P. martensi*), merits special mention. Their report is chiefly of value in that it is accompanied by illustrations of stained gonad sections. It is possible to see that germ cell development in this species is very similar to that in *P. albina*. The authors noted that the production of sperm is a continuous process; they were also able to distinguish between oogonial mitoses and the early meiotic configurations of leptotene, zygotene, and pachytene. However, they noticed few maturation figures in the ripe ovary, and concluded that "the course of maturation of the oocyte takes place after ovulation". At first sight, this seems to agree with what happens in *P. albina*; yet their Plate 1, Figure 11 ("The ovary immediately before ovulation") clearly shows that the oocytes have experienced germinal vesicle breakdown, a feature which has never yet been observed within the gonad of *P. albina*.

It can be accepted that the two species differ in this respect. Germinal vesicle breakdown usually marks the end of prophase and the beginning of prometaphase; it is therefore surprising to find that Ojima and Maeki did not observe metaphase chromosomes in oocytes such as were illustrated. Possibly the maturation cycle is arrested again at prometaphase; this would explain why the first maturation division does not automatically follow germinal vesicle breakdown, but is delayed till fertilization occurs. However, it is also possible that the tiny metaphase chromosomes have been overlooked, for it is the experience of the present author that at such a time in the maturation of *P. maxima* oocytes the chromosomes are far from prominent.

VI. Acknowledgments

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EXPLANATION OF PLATES 1–6

A, cell type A; *B*, cell type B; *dd*, digestive diverticula; *ext ep*, external epithelium; *fw*, follicle wall; *fwc*, follicle wall cell; *m*, muscle; *r*, residual mass; *sf*, spent follicle; *vct*, vesicular connective tissue. Spermatogenesis: *d spg*, definitive spermatogonium; *s*, stem cell; *spc* 1, primary spermatocyte; *spg*, spermatogonium; *spt*, spermatid; *spz*, spermatozoa; *spz d*, degenerate spermatozoa; *t*, sperm tails. Oogenesis: *cy*, cytoplasm; *N*, nucleus (= germinal vesicle); *n*, nucleolus; *Nm*, nuclear membrane; *ooc* 1–4, oocytes 1–4; *ooc d*, degenerate oocyte; *ooc f*, free oocyte; *oog*, oogonium; *d oog*, definitive oogonium; *rs*, resorption sac.

PLATE 1

Fig. 1.—*i*, the inactive gonad; gonad follicles empty except for phagocytic cells, and surrounded by vesicular connective tissue.

Fig. 2.—Md_1, early development of the male follicle; shows gradation in size from stem cell to definitive spermatogonium; follicle free of phagocytic cells and residual gametes.

Fig. 3.—Md_1Mr_3, redevelopment of the male primordia, associated with resorption of residual spermatozoa from the preceding reproductive phase.

Fig. 4.—Md_2, early male development at the stage where definitive spermatogonia are multiplying rapidly and separating from the follicle wall.

PLATE 2

Fig. 1.—Md_3, intermediate stage of development of the male follicle showing how the definitive spermatogonia of Plate 1, Fig. 4, have given rise to spermatocytes (chromosomal configurations) and spermatids.

Fig. 2.—Md_3, another aspect, showing the continuous nature of spermatogenesis: spermatozoa have arisen from the spermatids of Fig. 1, and another batch of spermatocytes have formed.

Fig. 3.—Md_4, late development of the male follicle; there is still a substantial number of spermatocytes and spermatids, which will probably mature before spawning takes place

Fig. 4.—Md_5 (low magnification), the ripe male follicle.

PLATE 3

Fig. 1.—Mr_1, the first stage of testis regression; the follicles are beginning to empty by spawning.

Fig. 2.—Mr_1 (high magnification), showing how the sperm tails become directed toward the centre of the follicle during spawning.

Fig. 3.—Mr_2Md_3, the final stage of regression in which emptying of the follicles is completed by phagocytic resorption (note density of phagocytes); in this case, regression associated with redevelopment of the male primordia.

Fig. 4.—Phagocytes (type A), highly magnified to show granular nature of the cytoplasm.

PLATE 4

Fig. 1.—Fd_1 (pre-growth stage), early development of the female follicle showing oogonia, and oocytes with chromosomes in a condensed tangle (oocytes 1).

Fig. 2.—Fd_1, another aspect, showing oocytes 1 and the succeeding stage where chromosomes disentangle and occupy a larger area (oocytes 2).

Fig. 3.—Fd_1, another aspect, showing stem cell, a typical intermediate oogonium, and oocytes 2, but no oocytes 1.

Fig. 4.—Fd_3 (early growth stage): the young oocyte grows in size (oocytes 3–4), becomes attached by a broad base to the follicle wall, and the densely staining nucleus begins to clear.

PLATE 5

Fig. 1.—Fd_4: ripe oocytes are being freed into the lumen, and their nuclei have become much lighter than the cytoplasm.

Fig. 2.—Free oocytes, highly magnified, showing structure of nucleus and nucleolus.

Fig. 3.—Follicles of the same gonad at various stages of development: top, Fd_4; centre, Fd_1; bottom right, Fd_3.

Fig. 4.—Part of the follicle wall showing the typical occurrence of oocytes 1 in the interstices between large oocytes.

PLATE 6

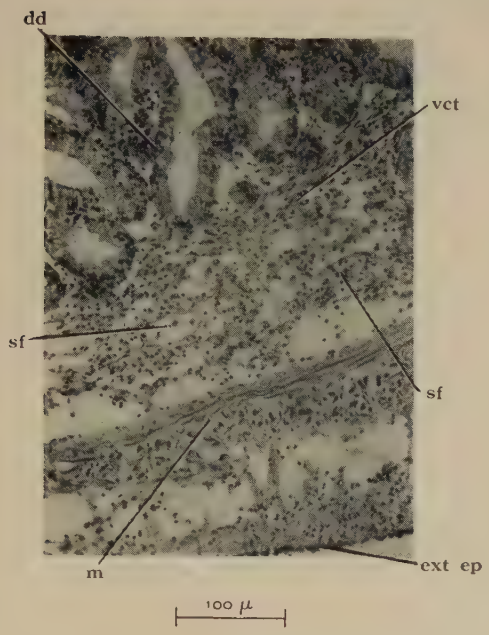
Fig. 1.—Fr_2: spawning has taken place and the residual oocytes are being resorbed by means of a series of "resorption sacs" surrounding each one.

Fig. 2.—Resorptive tissue magnified to show how it consists of individual phagocytic cells (usually type B).

Fig. 3.—Fr_2, another aspect, showing a slightly different resorptive "tissue" and illustrating the manner in which oocyte membranes break down during resorption.

Fig. 4.—Fr_3, final stage of regression—only an occasional oocyte in whole gonad; associated with initiation of a new reproductive phase.

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. II



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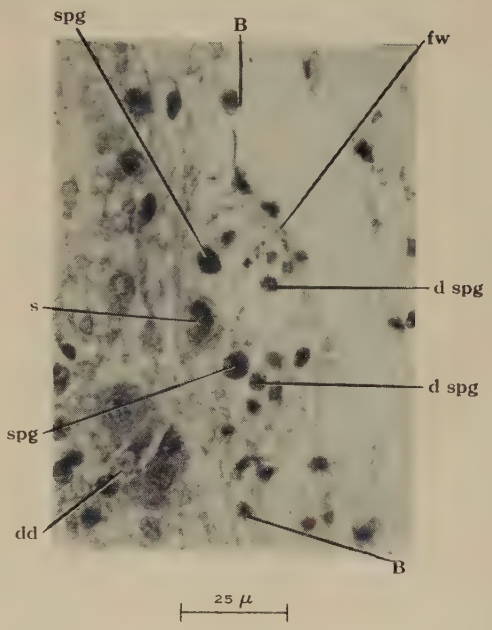

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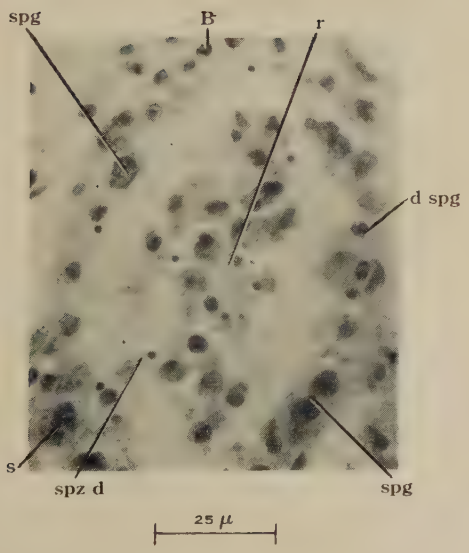

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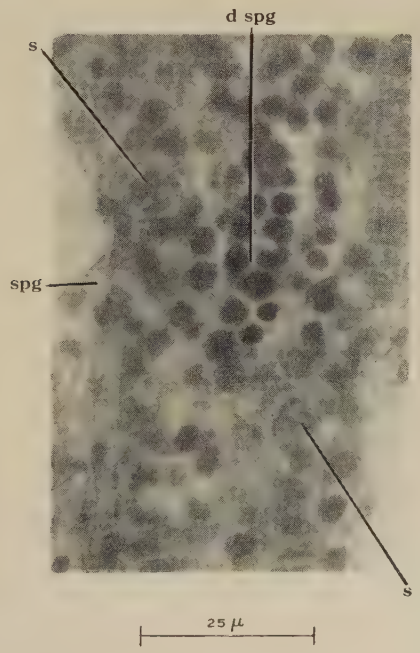

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REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. II

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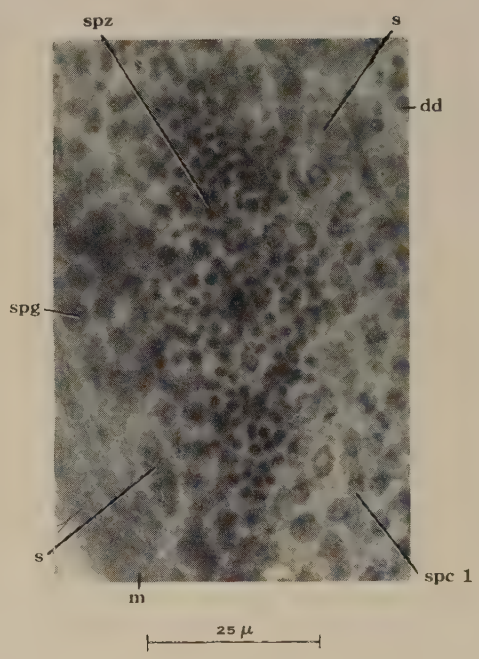

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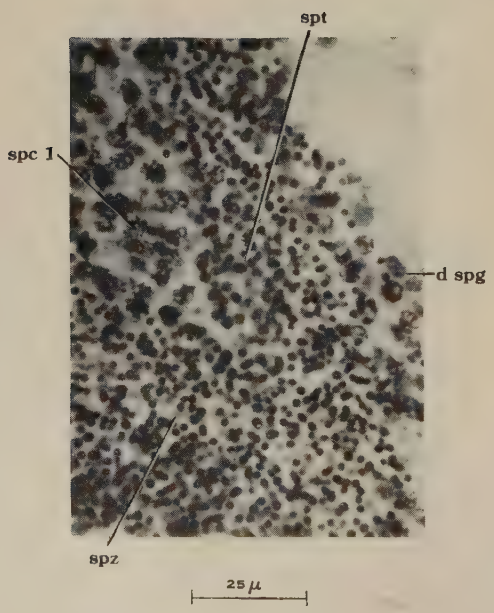

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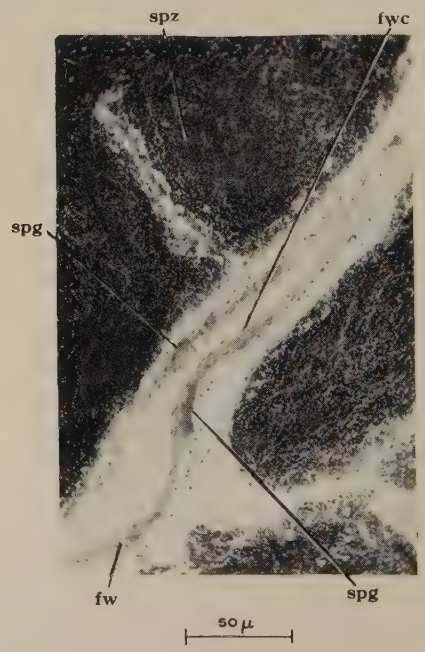

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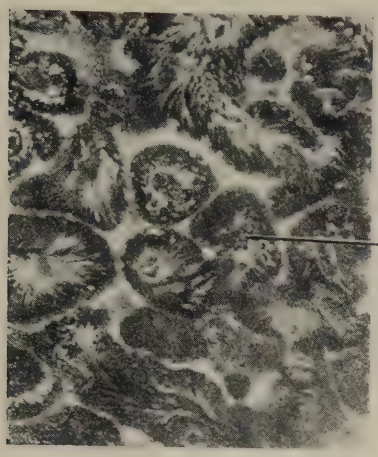
REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. II



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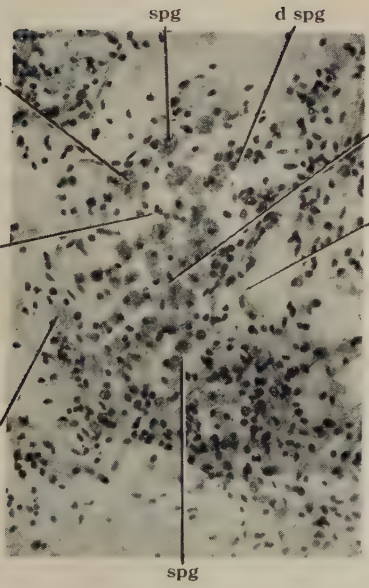

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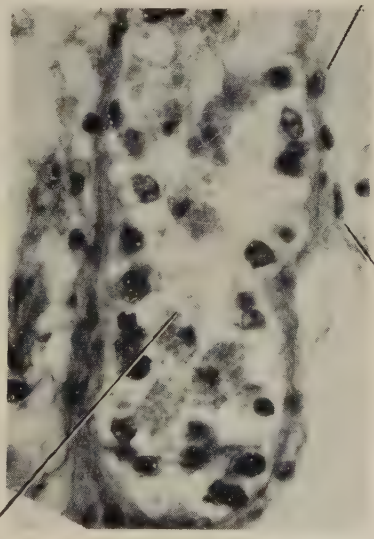

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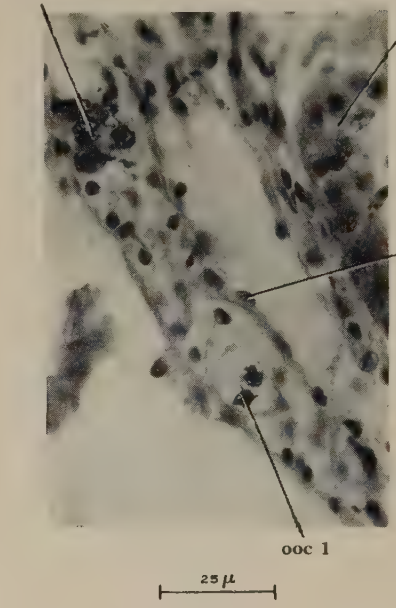

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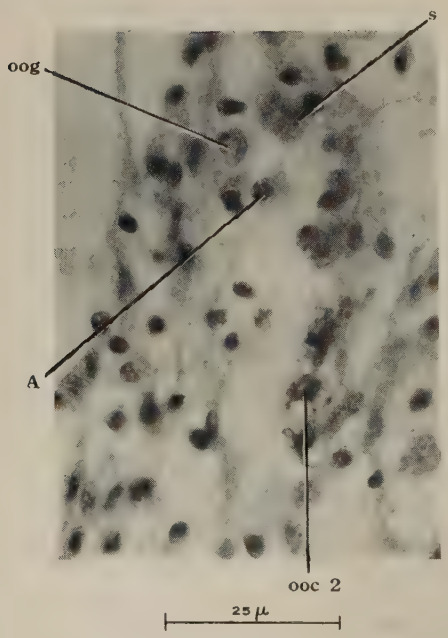

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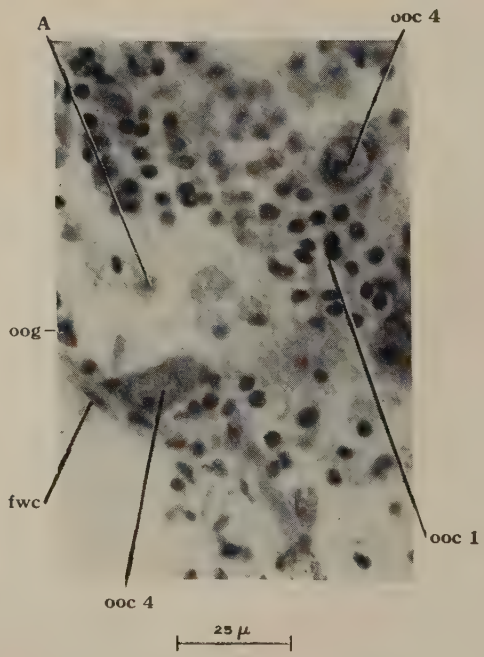

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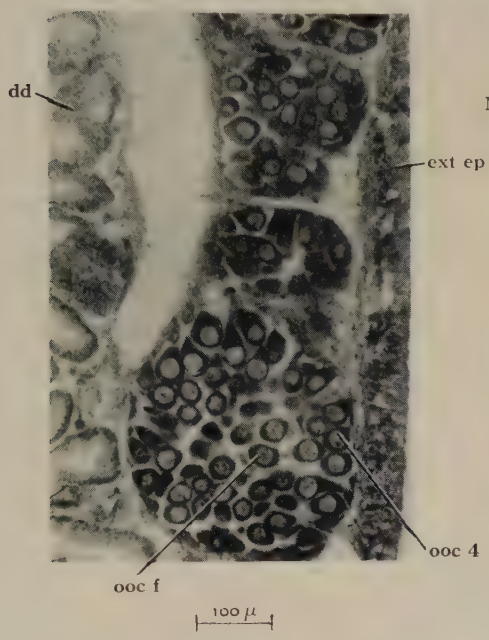

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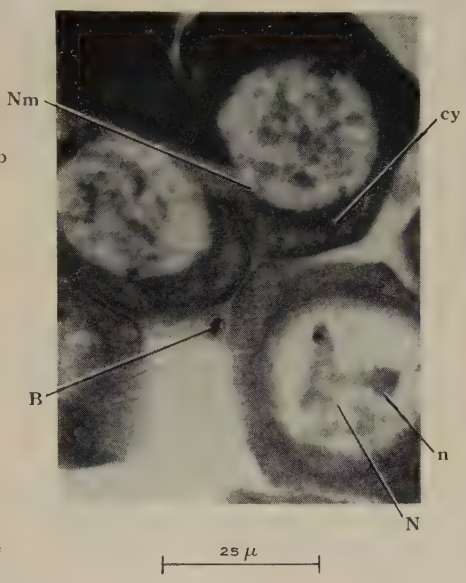

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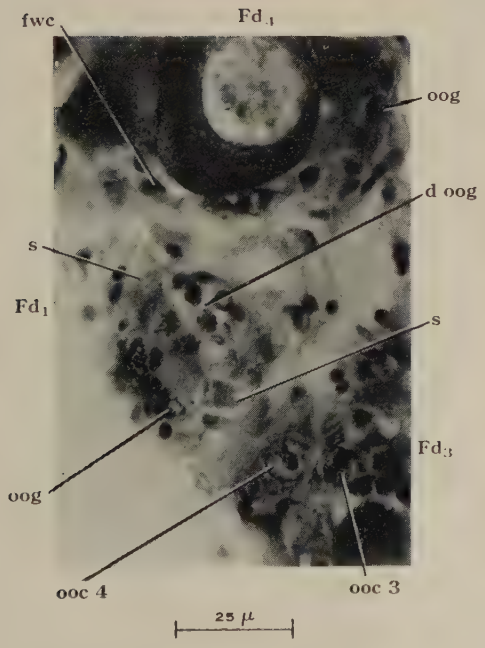

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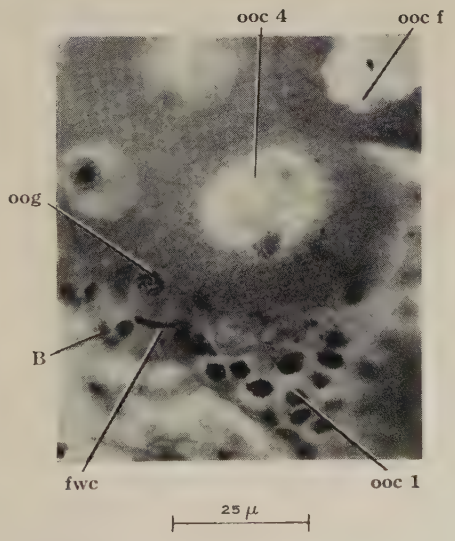

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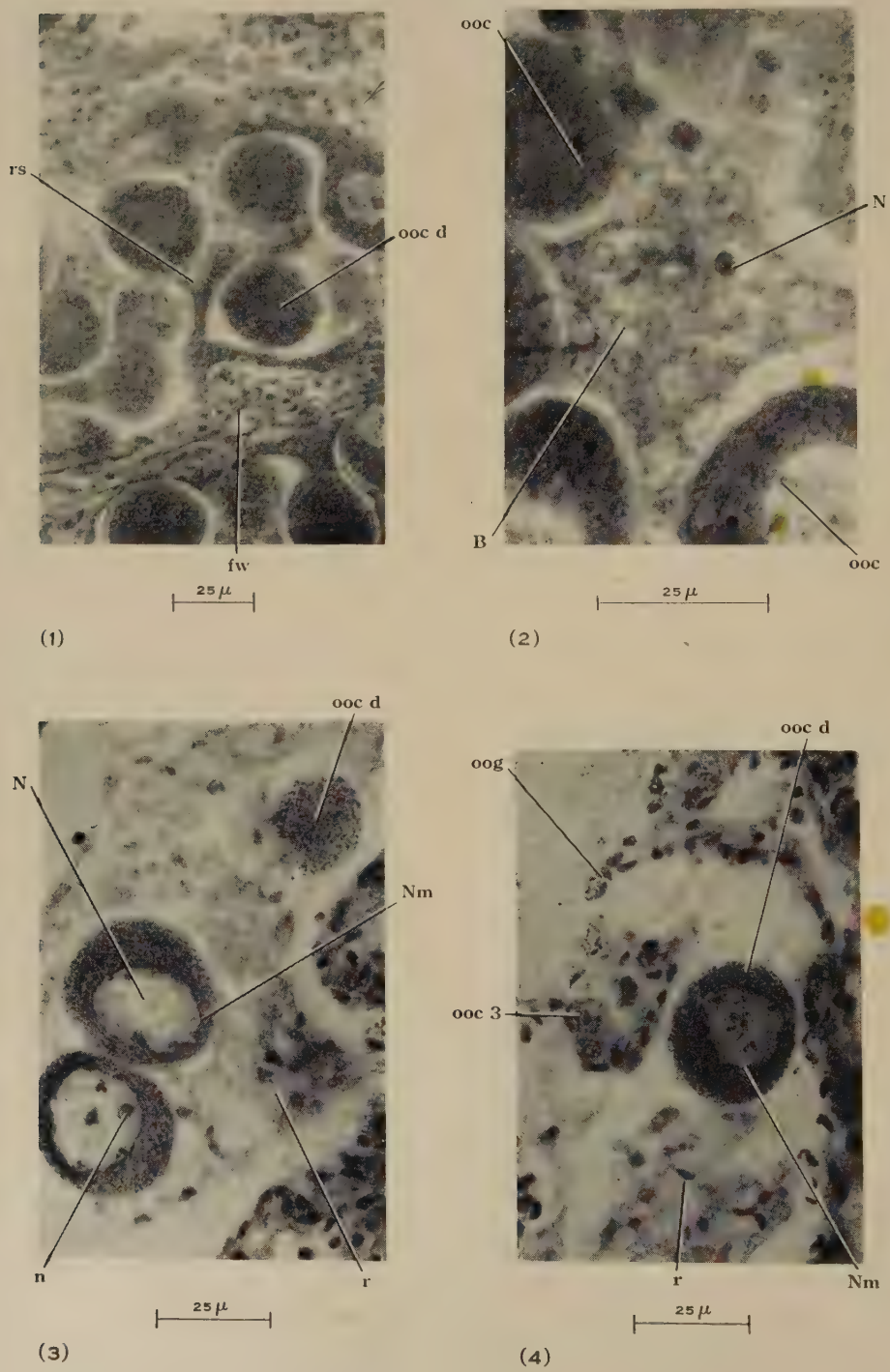
REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. II



GROWTH, PRODUCTION, AND SURVIVAL OF BROWN TROUT IN A LARGE FARM DAM

By A. H. Weatherley*

[*Manuscript received September* 23, 1957]

Summary

Two releases of yearling brown trout in a large farm dam were unsuccessful, the first because of the escape of the fish in a flood, the second for unknown reasons, though the fish which were recovered from both these releases had grown well. A third release, of 3300 yearlings, proved comparatively successful, for while the fish did not grow quite so well as in earlier years, 904 of them were recovered after 10 months. The total weight of fish in the dam as a result of the second and third releases represented a standing crop of 43·5 lb/acre (48·8 kg/hectare) or a production (for 10 months) of 21·8 lb/acre (24·4 kg/hectare). It was found that trout could become sexually mature in the dam, though they lacked suitable spawning grounds.

I. Introduction

In late 1951 observations were begun on a large farm dam in northern Tasmania, preparatory to releasing brown trout in it. The dam was constructed by forming an earth wall along the base of a slope in improved pasture land, and was filled from a channel from nearby Dairy Rivulet. The area was 3·7 hectare (9 acres) and the shape and depth contours are given in Figure 1. A controllable inflow allowed the maintenance of an almost constant water level, while outflowing water returned to Dairy Rivulet by way of pastures. Both outlet and inlet were screened soon after filling to prevent entry or exit of fish. Originally the bottom was grassed and this covering took about 6 months to decompose completely. Soon after the dam had been filled, aquatic plants from an irrigation channel were distributed in its shallows. They took root quickly and considerable quantities of *Myriophyllum propinquum* (Cunningham) and Cyperaceae were soon growing. The edges of much of the dam soon became lined with Cyperaceae, Juncaceae, and Restionaceae, while along the south-western shore these grew well out into the water.

II. Methods and Procedures

(*a*) *Hydrological*

A sampling station over the deepest part of the dam was occupied on eight occasions between April 1952 and January 1955, when water from the surface and bottom was collected in a brass bottle of 6-l. capacity.

The temperature of the water was taken at the time of each collection. Oxygen was estimated by Winkler's method. pH was measured colorimetrically in the field, bromothymol blue being used as an indicator. Total and fixed solids were estimated

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by the conventional analytical procedure of evaporating at 180°C for total solids, then igniting at 500°C for fixed solids. Samples were titrated with hydrochloric acid and results expressed as calcium bicarbonate alkalinity.

(*b*) *Biological*

(i) *Zooplankton.*—A silk net with a mouth of 30 cm diameter and with 40 meshes to the linear inch was towed over the course marked in Figure 1 in approximately 5 min, the catch being preserved with formalin. During the tows the mouth of the net was kept about $\frac{1}{2}$–1 ft ($\frac{1}{6}$ to $\frac{1}{3}$ m) below the surface.

Fig. 1.—Map of dam showing depth contours in feet (continuous lines) and course of zooplankton collections (dashed line).

(ii) *Bottom Fauna.*—A hand-operated grab sampler, covering 1 sq. ft. was used to collect samples, both from the open bottom and among plants: they were preserved with formalin in the field. The samples were handled in the laboratory as Weatherley and Nicholls (1955) have described.

(iii) *Fish.*—In April 1953, yearling brown trout were released in the dam, a random sample of 250 being weighed and measured. The dam wall was opened in March 1954, the dam thus being drained except for a small pool which was netted repeatedly until all the fish in it were removed. They were not replaced in the dam.

Following this, new screens of improved design were installed, and a concrete pipe through which the dam could be drained by raising a steel gate. After these improvements, more trout yearlings were released in June 1954, each fish having been marked by removal of its left pelvic fin. The fish were smaller than those of the earlier

release, as revealed by a random sample. In June 1955 the dam was drained and all fish were removed. They were returned to the dam after they had been measured and weighed.

Again in October 1955, yearlings were released, their size being similar to those of the first release, and each fish having had its right pelvic fin removed. The population was examined in August 1956.

TABLE 1

SUMMARY OF HYDROLOGICAL DATA

The mean values in this table are calculated from both surface and bottom data, which in almost all cases are very similar for any date

Data	Temperature (°C)	Oxygen (mg/l.)	pH	Total Solids (mg/l.)	Fixed Solids (mg/l.)	Bicarbonate Alkalinity (mg/l.)
Mean value		8·9	6·7	46	26	17·5
Range	6·6–20·7	7·0–10·6	6·2–7·1	32–61	20–34	9–20
No. of determinations	17	18	15	16	16	14

III. RESULTS

(a) *Hydrological*

The data, insufficient to depict seasonal or other trends, have been averaged and appear in Table 1.

(b) *Biological*

(i) *Zooplankton.*—Soon after the dam was filled in 1951 a rather large zooplankton population developed, mainly of Cladocera with some Copepoda. This persisted until January 1953, after which there was a decline. Values then appeared to remain low for 2 years, but in January 1955, 290,000 Cladocera were captured in a single tow. These changes are shown in Figure 2.

(ii) *Bottom Fauna.*—Before trout were released in 1953, ten samples were collected; three each from the northern and southern littorals and from among weed clumps, and one from the middle of the dam. Gastropoda (mainly Pulmonata) and Diptera (nearly all Chironomidae) then dominated the fauna, accounting for 47 and 35 per cent. respectively of the weight. Orthoptera, Hemiptera, Trichoptera, Ephemeroptera, Hydracarina, Hirudinea, and Oligochaeta were also found.

In 1954, seven samples were collected, the bottom fauna now lacking Gastropoda. Chironomidae had increased in numbers, and now comprised 91 per cent. by weight of the fauna. The position is summarized in Table 2. The standing crop was much the same in 1954 as earlier, the increased number of chironomids counterbalancing the disappearance of the gastropods. A single collection in January 1955 comprised almost 100 per cent. chironomids.

(iii) *Fish.*—Table 3 summarizes the releases and recoveries. It is seen that 36 of the fish released in April 1953 were recovered in March of the following year. Two

TABLE 2

CHANGES IN THE BOTTOM FAUNA

Year	Number per sq. metre		Weight per sq. metre (g)		Weight of Total Fauna per sq. metre (g)
	Gastropoda	Chironomidae	Gastropoda	Chironomidae	
1952	545	913	4·3	3·2	9·2
1954	0	3226	0·0	10·1	11·1

others were much larger and older than these 36 and therefore must have been in the dam before the latter were released and before the screens were installed. Another

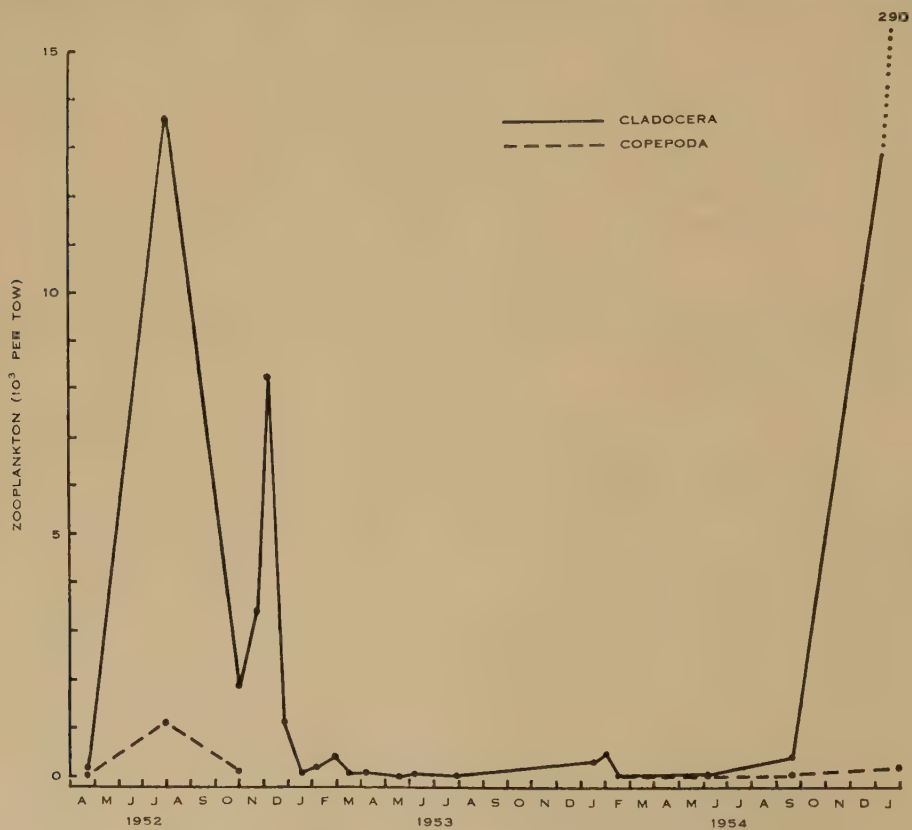

Fig. 2.—Zooplankton values in the dam. Note the large cladoceran population in January 1955.

trout was so small that it must have been spawned in Dairy Rivulet and passed through the screen while still very young. As Table 3 shows, a few other fish from this original release were collected in other ways during the year.

TABLE 3

SUMMARY OF RELEASES AND RECOVERIES OF BROWN TROUT

Releases				Recoveries				
Date	No.	Mean Length (cm)	Mean Weight (g)	Date	No.	Mean Length (cm)	Mean Weight (g)	Remarks
30. iv. 53	6827	9·5	9·4	5.viii.53	1	13·5	31·5	Taken in trap
				26. i.54	1	29·2	312·3	Found dead on shore
				25. ii.54	3	31·5	417·2	Netted; graball
				27. iii.54*	2	58·7	2750	Captured when dam drained; not of original release
					1	9·7	12·2	
					36	31·1	385	Captured when dam drained; remnant of fish released in 1953 (removed)
24. vi. 54	4140	6·5	2·6	30. vi.55	237	28·3	238	Survivors of 1954 release (replaced)
6. x. 55	3300	10·0	9·9	2.viii.56	130	33·3	365	Survivors of 1954 release
					904	24·8	140	Survivors of 1955 release

* 4·03 kg of eels were also collected on 27.iii.54.

Many more fish were collected as a result of the second release, but the stocking still could not be termed successful. A third release brought much better results than the earlier two, 27·4 per cent. being recovered in 1956 as against 5·7 per cent. in 1955 and 0·6 per cent. in 1954. The growth rate was slower for the last batch of fish released than for the earlier two and is doubtless related reciprocally to population density.

Ninety per cent. of the 130 trout taken in August 1956 as survivors of the release in June 1954 were either nearly ready to spawn or had already done so, though their spawning would be in vain because of the complete absence of suitable spawning grounds in the dam.

IV. Discussion

The water supplying the dam is low in mineral solids and for that reason alone plankton production in unlikely to be consistently high (Rawson 1951). However, zooplankton was always in evidence during some 2½ years and was more abundant than might have been expected. For example, during 1952 it was about 8–10 times as abundant as in Lake Dobson after enrichment; see Weatherley and Nicholls (1955). Meehean (1933) stated that "swarms" of *Daphnia magna* will appear in ponds on newly flooded pasture, apparently feeding on decomposing plant material. Perhaps this explains the rather large cladoceran population in 1952. The cause of the very large cladoceran population of January 1955 is not known, but presumably it must have been preceded and accompanied by algal abundance.

The quantity of bottom fauna, if standing crop may be taken as an index of production, was not unduly low. For example, Deevey (1941) gave values for 33 lakes with a mean of 92 kg per hectare. Only eight of his lakes had values exceeding those of the dam, which were 92 kg per hectare in 1952 and 111 kg per hectare in 1954. It seems quite likely that the disappearance of gastropods from the bottom fauna would be related to the feeding activity of the trout. The fact that chironomids were not similarly reduced might be explicable in terms of a higher reproductive rate.

Another important source of food for trout was aquatic Hemiptera, as was indicated by their presence in large numbers in two trout examined in February 1954, though their high mobility made them impossible to evaluate.

Section III(*b*)(iii) showed that the first two releases of trout failed, though actual growth rate was good in both years, this indicating adequate food. It is believed that the poor recovery of trout in 1954 was caused mainly by the floods of the 1953 winter. Sudden flooding caused water to flow around the sides of the screens and fish were apparently able to escape. Moreover it is probable that the two large trout among the 1954 recoveries consumed many 1953 yearlings, while eels could also have preyed on them. In 1954–55 fish could not have escaped, since the screens were improved and no heavy rain fell, and in 1955 no eels were found. In the search for possible lethal factors during 1954–55 temperature must be considered, and during the summer of 1954–55 the mid-water temperature reached 25°C. as revealed by a maximum-minimum thermometer. This is several degrees lower than the temperatures dangerous to brown trout (Needham 1938; Black 1953); moreover very few dead fish were seen despite weekly inspections by the owner during the summer. Since it is apparently impossible

to explain the heavy mortality of 1954–55 except in terms of some uncertain form of predation, it will be more profitable to examine the performance of the trout released in 1955 and assume that this gives a truer picture of the productivity of the dam.

Allowing for the weight of the fish released in 1955 and of those of the 1954 release, which were replaced after weighing and measuring, it has been calculated that from October 6, 1955, to August 2, 1956, production was of the order of 21·8 lb/acre (24·4 kg/hectare). In connexion with this calculation, it should be stated that the weight of the trout which were survivors of the 1954 release and which were replaced in the dam in July 1955 would have changed a little by early October, the time when the next batch of yearlings was released. However, this is the time of year of minimal change of weight for trout in Tasmania, and it is unlikely that the difference would be significant; any slight increase would be likely to be offset by the mortality which would have occurred. It has therefore been assumed that the total weight of these fish in October was the same as in June. It must further be mentioned that the mean lengths and weights in Table 3 are based on a sample of 249 fish, not the whole population of 1034. For this reason the production was slightly higher than would be estimated from the data in the table, since the total weight of the remaining fish in the population proved to be slightly greater than expected on the basis of the mean values for the sample. However, this amounted to a difference of only about 1·2 lb/acre (1·3 kg/hectare) and is quite insignificant in the present instance.

Of the yearlings released in 1955, 27·4 per cent. were recovered in 1956. However, the question arises whether, even in 1955–56, there were sufficient fish to utilize the available food most efficiently—that is, was production maximal? The growth rate of these fish, while still good, was distinctly slower than that of the fish of the two earlier releases. This suggests that competition for food was more intense than formerly and this view is strengthened by the fact that while survivors of the fish released in 1954 grew well in 1954–55, those remaining in 1955–56 grew poorly by comparison. It is concluded that while it is possible that production might have been greater if the population density had been higher, mean growth rate would certainly have decreased. So even if a larger population could have utilized food more efficiently it is not certain that this would benefit anglers if it meant an appreciably smaller mean fish size.

Data on standing crops or production of trout in unenriched "natural" lakes or ponds are very scarce. M'Gonigle and Smith (1938) poisoned a small (6-acre) trout lake with rotenone and collected the fish, finding a standing crop of 8·4 lb/acre (9·4 kg/hectare), while on the basis of a mark-recapture method Robertson (1947) reported a standing crop of about 44 lb/acre (49 kg/hectare) for a mountain trout lake. Schneider and Griffiths (1943) combined the techniques of fishing and poisoning to obtain a production value of 46·5 lb/acre (52 kg/hectare) in 14½ months for an artificial pond in Oregon. The stocking rates used by them were much lower than in the present case, when the standing crop was 43·5 lb/acre in August 1956, and production (for 10 months) 21·8 lb/acre.

V. Acknowledgments

This work was carried out on the property of Mr. L. F. Clarke of Chudleigh, Tasmania, and thanks are due to him for his interest and cooperation.

Mr. H. V. Jones, Chief-of-Staff of the hatcheries of the Salmon and Freshwater Fisheries Commissioners, and members of his staff gave valuable assistance in draining the dam and collecting trout. The Tasmanian Government Analyst and his staff were responsible for the chemical analyses.

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THE TASMANIAN TROUT FISHERY

III. THE RIVERS OF THE NORTH AND EAST

By A. G. Nicholls*

[*Manuscript received September* 23, 1957]

Summary

The study of the daily catch from the North and South Esk River systems, as derived from anglers' returns, shows a general fall which appears to be statistically significant in all rivers except the Meander. It appears to become increasingly important from west to east. It is accompanied by a fall in the annual catch per angler which is closely correlated with an increase in the number of licences issued, from which it might appear that these streams are being fished to their full capacity. A study of the mean lengths of fish at capture does not show any decrease compatible with overfishing, and there has been no increase in growth rate, which might be expected under conditions of overfishing. The age distribution of fish caught by anglers does not indicate any decrease in the proportions of older fish. A personal canvass of 53 anglers in one district showed a mean total catch per angler of 259 fish, whereas the figure derived from anglers' returns for the same season was 20 fish per angler. It is concluded that the apparent decline in catching rate was due to the returns from anglers being unrepresentative. No correlation was found between the catches by anglers and the fish available to them as a result of stocking these streams.

I. Introduction

The fishery in the rivers of the north and east of Tasmania will be treated in the same way as that for the North-West Region, described in the general introduction given in paper I of this series (Nicholls 1957*b*). Detailed results have been published (Nicholls 1957*a*) of which this is a condensation dealing with the fishery of the South and North Esk River systems. These two rivers discharge independently into the Tamar estuary at Launceston. Information from the several rivers which flow north into Bass Strait, or east into the Tasman Sea, is insufficient for inclusion here.

II. The South Esk River System

(*a*) *Environmental Characteristics*

The South Esk River system occupies an area of about 3500 sq. miles. It is divisible into three subsystems based on the main river and its two major tributaries. From west to east the subsystems are the Meander, the Macquarie, and the South Esk above the point of entry of the Macquarie. Each has numerous tributaries of varying importance.

The Meander River rises in Lake Meander at a height of over 4000 ft on the northern edge of the Central Plateau. Its initial descent is rapid, including a fall of

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about 500 ft at one point, and during the rest of its course of about 40 miles it receives several minor tributaries. Its mean gradient over this section is about 2 per mille (10 ft/mile), and the area of its basin is about 600 sq. miles. It joins the South Esk at Hadspen, about 10 miles south-west of Launceston.

The headwaters of the Macquarie River are in Tooms Lake and adjacent country lying to the south-east of Ross. It receives several tributaries in this area, but the

TABLE 1

MEAN DAILY CATCH PER ANGLER FROM SOUTH ESK RIVER SYSTEM

Season	Number of Anglers	Number of Fish	Number of Days	Fish per Day
1945–46	15	418	142	2·9
1946–47	25	1241	302	4·1
1947–48	26	1100	304	3·6
1948–49	12	417	147	2·8
1949–50	42	1453	482	3·0
1950–51	41	1056	344	3·1
1951–52	22	361	134	2·7
1952–53	28	334	163	2·0
1953–54	22	410	161	2·5

first of importance is the Elizabeth River, which drains Lake Leake and joins the Macquarie near Campbelltown. The Lake River, which drains Arthur's Lakes on the east side of the Central Plateau, joins the Macquarie about 12 miles above Longford, at which town the Macquarie flows into the South Esk. The Macquarie and its tributaries drain the south-western part of the South Esk basin, an area of about 1500 sq. miles. Its total length is about 100 miles, its mean gradient over the last 60

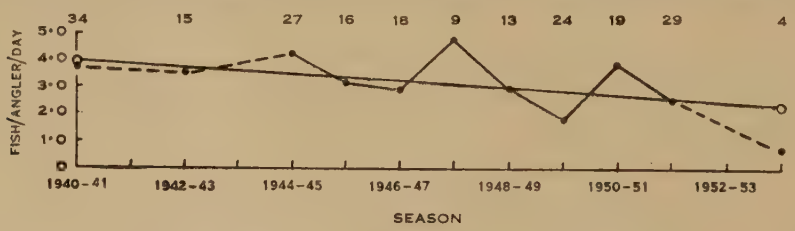

Fig. 1.—Mean daily catch by one angler from the South Esk River system during 14 seasons. The number of days spent fishing in each season is given above the graph.

miles being about 1 per mille. For most of its course it is a slowly moving stream, composed of a series of long deep pools joined by short stretches of shallow water. It meanders through agricultural land and is subject to considerable flooding in winter.

The South Esk River rises on the slopes of Ben Nevis, flowing in a general south-easterly direction at first, later changing direction to west and north to reach Launceston. After its initial rapid descent from the headwaters the mean gradient is about 2 per mille. It has a total length of about 100 miles and the area of the basin drained

by this subsystem is about 1400 sq. miles. In its lower reaches it pursues a very winding course and is subject to winter flooding.

Apart from isolated patches of highlands up to 5000 ft, the greater part of the basin of the South Esk River system lies below 2000 ft, and about one-half is below 1000 ft. The average annual rainfall for most of the area is 30 in., reaching higher figures only in the headwaters of the South Esk and Meander. The average monthly flow over a period of 50 years for the South Esk at Launceston was 2435 cu. ft/sec (range, 97 to 23,177). Apart from the city of Launceston there are no large towns comparable with those of the north-west coast, and nowhere does the population exceed 16 per sq. mile except within the boundaries of the numerous country towns.

TABLE 2

MEAN LENGTHS OF FISH FROM MEANDER, MACQUARIE, AND SOUTH ESK SUBSYSTEMS

Season	Meander Subsystem		Macquarie Subsystem		South Esk Subsystem	
	Number of Fish	Mean Length (in.)	Number of Fish	Mean Length (in.)	Number of Fish	Mean Length (in.)
1949–50	408	11·9	308	13·9	445	12·4
1950–51	512	11·4	230	13·4	316	12·4
1951–52	190	11·9	75	12·8	97	12·7
1952–53	146	11·9	86	13·8	111	13·6
1953–54	174	11·6	107	13·6	61	12·0
1949–50 to 1953–54	1430	11·7	806	13·6	1030	12·5

(b) *Results and Discussion*

(i) *The Daily Catch.*—The data for this river system are summarized in Table 1. This shows that there has been a decline in the number of fish taken per angler per day, and statistical analysis shows significant differences between seasons. A study of the data for the three subsystems separately shows that in the Meander there was very little variation and this was of the magnitude of the sampling error only. In the Macquarie stability was shown for the first 7 years, with a fall during the last two, and for the whole period no significant difference was found. In the South Esk subsystem considerable seasonal fluctuations occurred, and the differences were statistically significant, showing a general downward trend.

It has been possible to examine the diary of one angler, a resident of Launceston whose record of fishing in the rivers of this district covered a period of 14 seasons starting in 1940–41. The summarized data from this diary are illustrated in Figure 1. Statistical analysis shows that the differences between the means are significant at the 5 per cent. level only. The regression line fitted to the points shows a slight downward

trend. There is no indication of any acceleration in the rate of fall in the last nine seasons when compared with the earlier years.

(ii) *Fish Lengths.*—Over 3400 fish were measured from the rivers of this system during the last five seasons, and the results are given separately for each subsystem in Table 2. Statistical analysis of the data from the Meander showed that the differences are significant at the 1 per cent. level, but that this was due to the inclusion of small samples with considerable variability from one tributary; when these were excluded no significant difference was found. There was no significant difference in

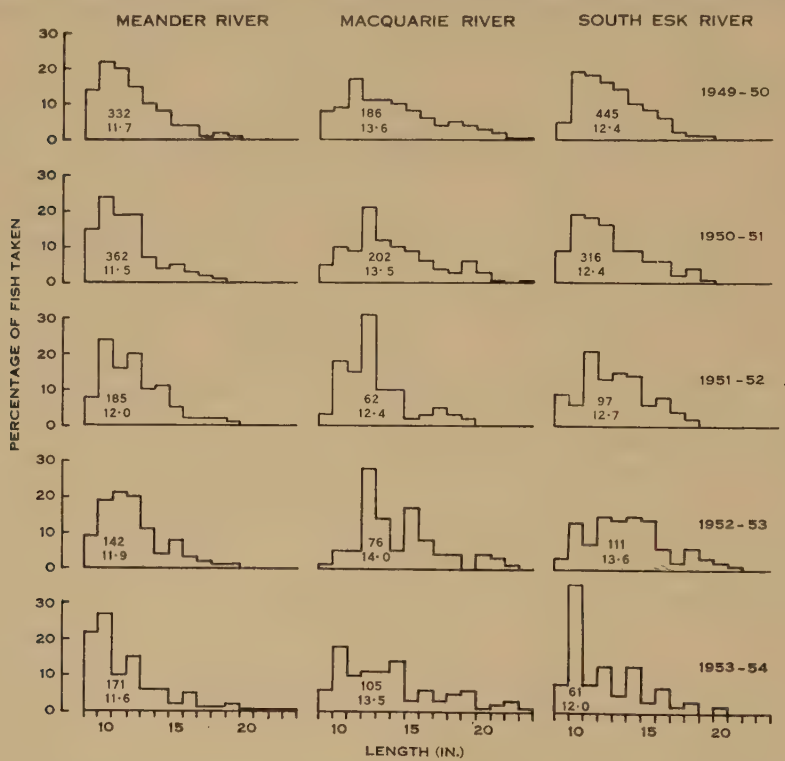

Fig. 2.—Percentage size frequency histograms of fish taken by anglers from the Meander, Macquarie, and South Esk Rivers during five seasons. The absolute numbers of fish measured and the mean lengths of fish are given in each case.

the mean lengths of fish from the Macquarie subsystem. The lowest mean length, which occurred in 1951–52, was due to the absence of any large fish of 20 in. or over; for the other four seasons the percentages of such fish were 6·8, 4·3, 7·0, and 7·5 respectively. Fewer fish were recorded in this season than in any other but it had the highest daily catch rate for the last five seasons. Fish measurements from the Elizabeth River have been excluded since the fish were distinctly smaller than those of the rest of the subsystem. The mean length of 163 fish over the five seasons from this tributary was 12·4 in., and there was no significant difference between seasons. In the South Esk subsystem the majority of measurements came from fish taken in

the main stream. Differences between the means are quite significant, but if the figures for 1952–53 are omitted they are not significant. This exception can reasonably be regarded as due to a sampling effect.

Table 2 shows that in no case was there any evidence of a constant downward trend, such as would have been expected if there had been a marked depletion of the population during the period. There are, however, fluctuations which can best be examined in percentage size frequency histograms, which have been plotted for the Meander, Macquarie, and South Esk subsystems in Figure 2. In general, the changes in mean lengths are parallelled by changes in composition of the population. In the Meander, for example, in 1951–52 and 1952–53 when the means stood at their highest there were smaller than normal proportions of fish in the smallest size groups, and the fall in the following season was accompanied by a rise in the proportion of small fish. The Macquarie shows stability during the first two seasons, an increase in the proportion of small fish in 1951–52, and a considerable decrease in this group in the next season, followed by a return in 1953–54 to the conditions found in the first two seasons. In the South Esk there was stability during the first two seasons, a decrease

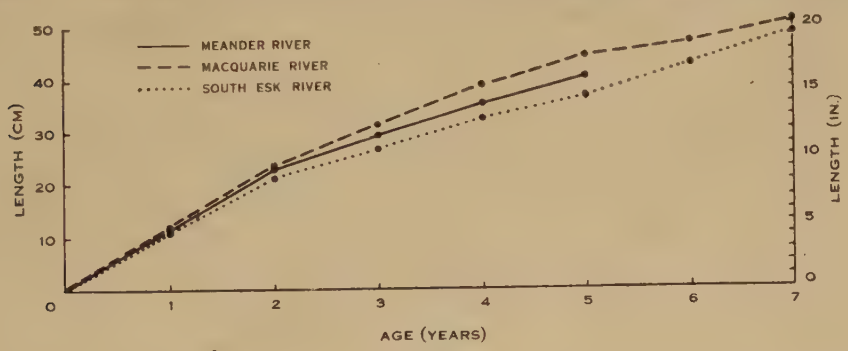

Fig. 3.—The growth of fish in the Meander, Macquarie, and South Esk Rivers.

in the proportion of smaller fish in the third season, a further decrease in 1952–53, and a marked increase in the final season. It may be noted that some of the data presented in this figure show an even-number bias, most evident for the South Esk in 1953–54, which suggests that some of the fish measurements were not made with care.

It is possible that the changes in the proportions of small fish may be related to varying success in survival of particular year classes, or to the rate of stocking with hatchery fish. This is considered in Section II(*c*).

(iii) *Growth and Age.*—From this system, 652 scale samples were available for examination: 214 from the Meander, 251 from the Macquarie, and 187 from the South Esk. The mean lengths of fish at each year of age are shown in Figure 3, for the three subsystems. Detailed analyses of the data from different sources within each subsystem show minor differences in growth rate, but it has been concluded that for present purposes these can be ignored and the data pooled to express mean values for the growth rate in each subsystem. No data were available for the Elizabeth River.

Statistical analysis of the mean lengths at each year shows significant differences between the three subsystems. From L_1 to L_5 the differences are highly significant; thereafter they are not significant, but only a few fish were available for comparison. Figure 3 shows that up to 5 years of age the best growth is found in the Macquarie and the poorest in the South Esk, and that the Meander fish are intermediate. Growth in the Meander and Macquarie is similar, but at L_3 the difference in mean length is quite significant; at L_2 and L_4 it is significant only at the 5 per cent. level; and at L_1 and L_5 it is not significant. These differences in growth rate will affect the ages at which fish are caught in these rivers, and this is discussed in Section II(*b*)(vi).

(iv) *Condition.*—The mean values for the condition factor of fish from these subsystems, based on fish recorded for scale reading, were: Meander, 1·33; Macquarie, 1·10; and South Esk, 1·28. In each case the tendency for condition to decrease with increasing age was evident. The fact that condition was better in the Meander and South Esk than in the Macquarie would appear to be in conformity with the general principles laid down by Huet (1954) in his study of stream gradients in relation to their habitation by fish. He has shown that most streams can be divided into four zones, of which the uppermost with the steepest gradient is occupied by trout, the next two being classified as "grayling" and "barbel" zones, while the lowest is the "bream" zone.

It would seem that in Tasmania these principles have a limited application since the majority of species listed by Huet are absent from these waters, and the only ones present have been introduced. Trout appear to have occupied the whole of the streams at the expense of the indigenous species, which have been unable to compete successfully and now just hold their own. Other introduced species (perch and tench) appear to inhabit the same stretches of water as the trout, except in the upper zones, and do not appear to have established any ascendancy even in those reaches which should provide conditions more suited to them. The application of Huet's principles here may possibly be seen in the condition of trout from different sections of the same system. The gradient and width of the Meander and South Esk are such as to fall within Huet's trout and grayling zones, and in these the condition factor is higher than in the Macquarie, which clearly belongs to the barbel zone. It should be noted that trout in Tasmania occupy not only the three upper zones but also the lowest or bream zone, in which the width is greater than 25 m and the gradient is below 0·5 per mille; in fact, trout occur freely in the estuaries for at least part of the summer.

(v) *Tagged and Marked Fish.*—During the last 5 years over 21,000 marked fish have been released in this river system, of which 270 were tagged. Evidence is available that anglers have marked fish on their own initiative during the period of this investigation, so that it has been necessary to accept as definite only those recaptures which corresponded both in mark and age to released fish. Of the marked fish, six probable and one possible brown, and three rainbow trout have been accepted; one of the tagged brown trout was reported. In some cases considerable distances appear to have been travelled before recapture, and five of these indicate that over the course of a few years released fish had become dispersed throughout the system. The exceptions were two brown trout released in the Macquarie in 1952 and recaptured at the same place in the 1955–56 season, two rainbow trout released in a tributary of the Macquarie and

recaptured at the same place about 4 months later, and one released in the upper reaches of the South Esk in 1952 and recaptured at the same place 2 years later. The single tagged fish reported was a brown trout yearling released in a tributary of the Macquarie in September 1951, taken a few weeks later by a 2½ lb brown trout, and disgorged partly digested when the larger fish was landed by an angler. Thus, of the 11 acceptable recaptures six were taken at or near the place of release and five had travelled considerable distances.

Movement of this nature is not in accordance with the conclusions of Allen (1951), who found that in the Horokiwi River there was relatively little movement of tagged fish and that the great majority "were recaptured either at the point where they had been liberated or within a few hundred feet of it". However, his tagged fish were removed from the population for tagging and returned to the same stretch of water whereas in the present investigation the marked fish were additions to the population. The maximum period of freedom in the Horokiwi fish was 333 days, whereas three of the South Esk fish were free for 3–4 years. Allen found no seasonal movement, and tagged fish "recaptured while spawning were all taken at or near the point of liberation". The greatest distance travelled by any fish in the Horokiwi was about 4½ miles upstream in 195 days; the majority of those covering long distances moved upstream, but one appears to have moved several miles downstream in 51 days. In the present case, if the possibility of these fish having been marked by anglers can be excluded (by no means certain), for brown trout the movement of the two 2-year marked fish represents a distance of over 50 miles upstream in one case, and 20 miles downstream followed by a similar distance up a tributary in the other, within about 1 year. For two of the 4-year fish the distance travelled was about 10 miles upstream in 3 years, while the other two were found near the place of release 3 and 3½ years later; the fifth would have travelled at least 40 miles upstream in 4 years. The rainbows, which were almost certainly those marked in this investigation, apparently did little or no travelling even after 2 years.

Although Allen found spawning fish close to the point of release the difference in the size of the two rivers and the greater time of freedom in the South Esk fish would have allowed, and increased the likelihood, of considerable seasonal movement. The marked yearlings liberated in the South Esk were mostly released in the lower stretches of the river where there is a considerable volume of water, not very suitable for spawning. There would thus have been some inducement to move. There is evidence that in the larger rivers of Tasmania a distinct spawning migration occurs, and is followed by a return to the lower reaches of the river or to the estuary. Thus the older fish taken many miles upstream could have made several such migrations during their period of freedom.

(vi) *Mortality Rates.*—The results of the scale readings have shown that the growth rates in different parts of this river system are significantly different, and it follows that the allocation of fish measurements made by anglers into age groups must be done for each subsystem separately. The mean lengths at capture of fish recorded by anglers (Table 2) show that the largest fish were taken from the Macquarie, and the smallest from the Meander. Figure 3 shows that the growth rate in the Meander is better than that in the South Esk, but there is no conflict here. The data from

anglers' catches must be regarded as representing the population, and the mean lengths at capture of the samples of fish used for age determination show the same order as that given in Table 2. It may be inferred that the fishery in the Meander is mainly on the younger fish. It is therefore permissible to treat these groups as three separate units for apportionment into age groups from scale readings from the appropriate subsystems, as described earlier (Nicholls 1958).

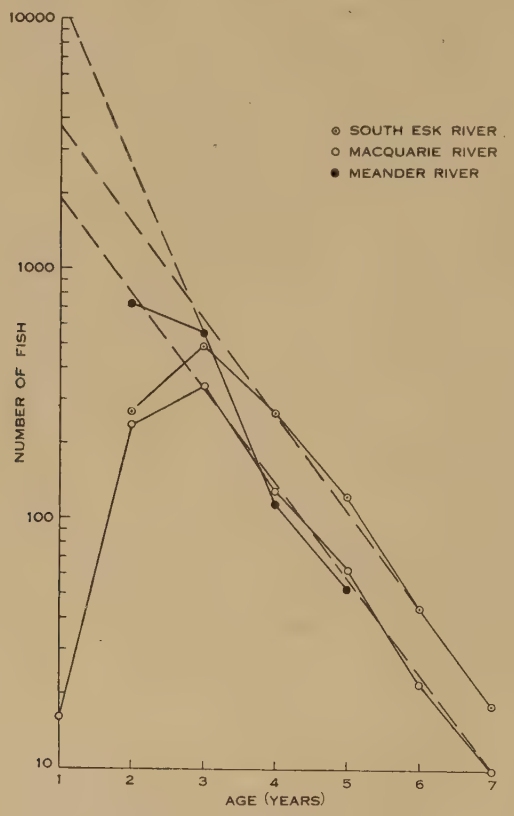

Fig. 4.—Catch curves for the Meander, Macquarie, and South Esk Rivers.

The numbers have been plotted logarithmically against fish ages in Figure 4. From these it will be seen that the slopes of the descending limbs are approximately the same for the Macquarie and South Esk. Straight lines drawn through the points on the right limbs of the curves are practically parallel, which indicates similar mortality rates, and these are extrapolated in order to estimate the proportions of 2-year and 1-year fish which were likely to have been taken. The average mortality rates for these two subsystems can be calculated at 59 per cent. The Meander subsystem yielded quite different results. There were no fish over 5 years of age in the samples for age determination, so that information on the mortality rate after the fifth year is lacking. It appears to be quite high, about 80 per cent., from the third to the fourth years, and to fall to about 55 per cent. from the fourth to the fifth. This

suggests that if it were more complete the whole curve might be concave, indicating a high initial mortality decreasing with age, in which case the mortality for the second to third years would be in excess of 80 per cent. On the other hand, the absence of fish over 5 years of age suggests a mortality increasing with age. It has been assumed that the mortality from the second to third years is the same as that from third to fourth, and the line was extrapolated accordingly to arrive at an approximate figure for the numbers of 2-year fish. The higher mortality rate indicated for young fish in this subsystem suggests that the fishery is mainly centred on the younger fish.

The different growth rates found in the three subsystems will affect the proportions of young fish protected by the minimum legal length. In the Macquarie subsystem, where the growth rate was highest, all of the 3+, about 30 per cent. of the 2+, and less than 1 (0·8) per cent. of the 1+ fish were takable. In the South Esk subsystem, where it was lowest, only about 77 per cent. of the 3+ fish, 17 per cent. of the 2+, and none of the 1+ fish were takable. For the Meander subsystem with an intermediate growth rate, there is some uncertainty, but if the mortality rate during the third year is no greater than that in the fourth (as assumed) it follows that all of the 3+, about 28 per cent. of the 2+, and no 1+ fish are takable. These figures are close to those of the Macquarie, and the growth rate in these two is similar. It will be noted that no 1+ fish were taken and the number of 2+ fish was very high in proportion to the 3+ when compared with other rivers. The large proportion of young fish taken in this river and the apparent absence of fish over 5 years of age suggest that this river is more heavily fished; it is shown below (Section II(*b*)(viii)) that this is probably true. In the total of nearly 1200 measurements, only five fish were 20 in. or more, and while one or more could have been older than 5 years, their lengths fall within the range of 5-year fish.

These figures will be of significance in studying the survival rate for stocking with hatchery-reared fish. Allen and Cunningham (1957) have drawn attention to the possibility that catchability may increase with size. This would arise from the inherent selective nature of the fishery whereby larger fish occupy the more favourable sites and drive off competitors. The angler, again exercising selection, would thus be more likely to hook the larger fish. If this were so it would affect the accuracy of the mortality rates from natural causes, but it is doubtful if it has a practical application here since the mortality rates given express mortality from all causes, including angling. The data presented in Figure 2 might appear to support this hypothesis, since the proportions of fish among the smaller size groups represented in the catches are less than might be expected from a normal distribution, which indicates that they are less catchable. But it has been shown earlier (Nicholls 1958, Fig. 3) that the poorer representation of the smaller fish arises from the operation of the size limit whereby only the quicker-growing fish of the younger age groups, a relatively small proportion, enter the fishery.

(vii) *Annual Catch per Angler.*—Figures for the mean annual catch per angler are given in Table 3 for the system as a whole, and for each subsystem separately. While some fluctuation between seasons is evident, the general trend has been downwards. Statistical analysis shows no significant differences between the means for the Meander; differences significant at the 5 per cent. level for the Macquarie; at the 1 per

TABLE 3

MEAN ANNUAL CATCH PER ANGLER FROM THE SOUTH ESK RIVER SYSTEM

Season	Meander Subsystem			Macquarie Subsystem			South Esk Subsystem			South Esk River System		
	Number of Fish	Number of Anglers	Fish per Angler	Number of Fish	Number of Anglers	Fish per Angler	Number of Fish	Number of Anglers	Fish per Angler	Number of Fish	Number of Anglers	Fish per Angler
1945–46	580	8	72·5	128	8	16·0	428	11	38·9	1136	17	66·8
1946–47	258	16	16·1	162	12	13·5	876	15	58·4	1296	27	48·0
1947–48	148	10	14·8	426	10	42·6	822	21	39·1	1396	31	45·0
1948–49	156	5	31·2	245	7	35·0	72	6	12·0	473	12	39·4
1949–50	522	23	22·7	497	22	22·6	576	20	28·8	1595	47	33·9
1950–51	613	25	24·5	286	18	15·9	352	20	17·6	1251	45	27·8
1951–52	244	18	13·6	94	10	9·4	157	12	13·1	495	26	19·0
1952–53	176	14	12·6	155	13	11·9	140	21	6·7	471	34	13·9
1953–54	211	16	13·2	155	12	12·9	54	11	4·9	420	26	16·2
1945–46 to 1953–54	2908	135	21·5	2148	112	19·2	3477	137	25·4	8533	265*	32·2

*The total number of anglers fishing the South Esk River system is less than the sum of those fishing each subsystem, because the same angler may have fished in more than one river.

cent. level for the South Esk subsystem; and at the 0·1 per cent. level for the system as a whole. The means for the 9-year period show little differences between rivers, and that for the system as a whole is higher than those of individual subsystems because many anglers have fished in more than one subsystem.

The reliability of these figures may be open to question for several reasons. The rather high value for the first season was due to one return from the Meander recording the capture of 485 fish. Such a high figure has not been reported since, nor did this angler make any subsequent return during the period, though it will be shown below that similar catches have been taken from this river. When this catch is omitted the mean for this season falls to 13·6 for the subsystem and to 40·7 for the whole system.

TABLE 4

CORRECTED NUMBERS OF LICENCES ISSUED IN NORTH AND SOUTH ESK AREAS

Data	Season								
	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
No. of licences issued:*									
Total	1126	1358	1583	2232	2628	3207	3334	3066	3159
Corrected No.	1188	1433	1670	2355	2777	3383	3543	3238	3333
No. of returns received:*									
Total	19	30	35	13	55	53	35	39	28
South Esk	17	27	31	12	47	45	26	34	26
North Esk	9	18	17	3	23	17	16	16	9
Estimated numbers fishing:									
South Esk	1063	1290	1479	2174	2373	2872	2632	2823	3095
North Esk	563	860	811	543	1161	1085	1620	1328	1071

*Weekly and daily licences and returns are excluded.

(viii) *Estimated Total Catch.*—By the method described earlier (Nicholls 1958) estimated total annual catches have been calculated. The number of licences issued in each season is given in Table 4. These have been extracted from records in which they were grouped into four districts: north-west, north, north-east, and south. This grouping includes in the north-east district some centres which are within the basin of the South Esk system; corrections have been made for these, and for the proportions of licence holders fishing in the North and South Esk.

In Table 5 are given the estimated total catches for the system as a whole, together with the coefficient of variation, for each season. In computing these, allowance has been made for the two sources of variation: (1) in computing the mean catch per angler from anglers' returns; (2) in estimating from the returns the proportion of anglers fishing in this system. From these coefficients standard errors

have been calculated, the largest relative standard error being that of 1945–46, owing to the inclusion of the single large catch from the Meander referred to above.

The figures show a fall in the estimated total catch over the last five seasons, the means for the first four and last five being 71,250 and 59,000 respectively. This fall has occurred in spite of the marked increase in the number of licence holders, which rose in 1953–54 to nearly three times the number in 1945–46. The mean annual catch per angler, and hence the estimated total catch, will depend in part on the number of days spent fishing in each season. The relationship between these two factors is shown in Table 6; the figures for mean catch per angler differ from those given in Table 3 because in comparing these data, returns from which the number of days were omitted must be excluded. As was to be expected there is a close relationship between the total catch per angler and the number of days spent fishing, and it is clear that the lower total catches of recent years were due to a lower fishing intensity. This may have been

TABLE 5

ESTIMATED TOTAL CATCHES FOR SOUTH ESK RIVER SYSTEM

Season	Number of Anglers	Mean Number of Fish per Angler	Estimated Total Catch*	Coefficient of Variation	Standard Error*
1945–46	1063	66·8	71,000	0·437	31,000
1946–47	1290	48·0	62,000	0·221	13,500
1947–48	1479	45·0	66,500	0·151	10,000
1948–49	2174	39·4	85,500	0·304	26,000
1949–50	2373	33·9	80,500	0·184	15,000
1950–51	2872	27·8	80,000	0·184	14,500
1951–52	2632	19·0	50,000	0·274	13,500
1952–53	2823	13·9	39,000	0·224	8,500
1953–54	3095	16·2	50,000	0·362	18,000

*Adjusted to the nearest 500.

due, in part, to the attraction offered to anglers by the newly opened lakes (this is supported by the steady increase in the proportion of lakes licences issued during the last five seasons), and also partly to a lessened interest in making returns. During the last four or five seasons a large proportion of returns came from anglers who had not previously submitted returns, which suggests that they may have come from anglers who had not fished before.

There is some evidence to show that anglers who regularly take good catches seldom make returns. This comes from the Deloraine district, from fishing in the Meander River only, between Meander and Exton during 1950–51. A personal canvass of 53 regular anglers made at the end of that season yielded catches ranging from 50 to 728, totalling 13,736 with an average of 259 fish per angler. Some of these anglers fish almost every night of the season which, for an 8-month season, indicates a mean daily catch of about three fish for the highest individual catch. None of these anglers sent in

returns, except one in 1945–46 referred to in Section II(*b*)(vii). On the assumption that the figure for the mean catch per angler derived from the returns (19·7 for the Meander alone in 1950–51) represents the mean for all anglers other than those canvassed, the total estimated catch becomes 39,000 compared with 26,500 calculated for this river. It is almost certain that the higher figure is an underestimate, and the true figure could be greatly in excess of 40,000, which represents about 1000 fish per mile of stream between Meander and Hadspen.

This approach to an assessment of the annual catch suggests that the figures given in Table 5 are underestimated because of the absence of returns from anglers who fish regularly and normally take good catches. A similar canvass carried out for the 1955–56 season showed that 55 anglers took an estimated catch of over 7100 fish, with a mean of 129 per angler, the highest being 348. The intensity of angling in this district is such that 84 were counted in one evening along 2½ miles of river, or one to every 52 yards.

(ix) *Summary.*—A statistically significant decline in the daily catch per angler was found, but the analysis of one angler's diary over 14 years shows only a slight downward trend. Mean lengths of fish taken by anglers indicate different growth rates

TABLE 6

MEAN ANNUAL CATCH AND MEAN NUMBER OF DAYS PER ANGLER

Data	Season								
	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
No. of fish	27·9	49·2	42·3	34·8	34·6	25·8	16·4	11·9	18·6
No. of days	9·5	12·1	11·7	12·3	11·5	8·4	6·1	5·8	7·3

in different rivers but in no case was there any constant trend over five seasons. Changes in the composition of the catch are related to variations in the occurrence of large fish in a season's catch. Marked fish recaptured have indicated extensive movement of fish within the system except in the case of rainbow trout. Mortality rates are about 60 per cent. per annum in the Macquarie and South Esk, but are higher in the Meander at about 80 per cent. There are indications that this river is heavily fished, but not overfished. The annual catch per angler has shown a fall, and the estimated total catches are lower during the last five seasons than during the first four, but these changes are probably related to a fall in the number of days spent fishing. A canvass of anglers who had not made returns in one district showed that figures for annual catch per angler and total catch are probably considerably underestimated.

(*c*) *The Relationship between Total Catch and Survivors from Stocking*

As was shown earlier (Nicholls 1958), if the numbers of fish released in the rivers and the appropriate mortality rates for fish in these streams are known, it is possible to calculate the probable survival and the approximate numbers present in any

season. Different mortality rates have been found for the Meander subsystem and the rest of the South Esk system, and it has therefore been necessary to calculate the survivors for each river separately and sum the results. These are given in Table 7, in which allowance has been made for the fact that only about 30 per cent. of the 2-year fish and 1 per cent. of the 1-year fish are likely to be taken in the Meander and Macquarie Rivers, and 80 per cent. of the 3-year, 20 per cent. of the 2-year, and no 1-year fish are likely to be taken in the South Esk and Elizabeth Rivers. Under the stocking rate which existed between 1942 and 1954, released fish could have contributed nearly 10 per cent. of the fish taken (the mean ratio for the last seven seasons is 1:11), but this could have occurred only if all the released fish were accounted for in the total catches, a most improbable event.

A comparison between the age distribution of the population of fish taken by anglers with that of the survivors from stocking will show if any relationship exists. The percentage composition of each population is shown in Figure 5, in which the

TABLE 7

TAKABLE SURVIVORS FROM STOCKING IN RELATION TO TOTAL CATCH FROM SOUTH ESK RIVER SYSTEM

Data	Season								
	1945–46	1946–47	1947–48	1948–49	1949–50	1950–51	1951–52	1952–53	1953–54
Takable Survivors	1,417	866	5,166	10,026	7,600	4,672	4,631	6,011	4,864
Total catch	71,000	62,000	66,500	85,500	80,500	80,000	50,000	39,000	50,000
Ratio	1:50·1	1:71·6	1:12·9	1:8·5	1:10·6	1:17·1	1:10·8	1:6·5	1:10·3

percentage age distribution of fish taken by anglers is given above the central line and that of takable fish surviving from stocking below. If there were a close relationship these pairs of histograms should be approximately mirror images of one another. It is clear that this is not the case, though for 1952–53 there is a fairly close resemblance in the Meander and Macquarie Rivers. Figures for fish taken by anglers show little seasonal change whereas those for takable survivors from stocking show considerable seasonal variation. Statistical analysis shows no significant difference in age distribution between seasons for the Meander and Macquarie, and a difference significant at the 1 per cent. level for the South Esk, whereas the differences for survivors from stocking were very highly significant in all these rivers. The majority of fish in all three rivers were 2 or 3 years of age, with 2-year fish predominating in the Meander and 3-year fish in the other two rivers; this relationship does not hold for the survivors from stocking. In conformity with the growth rates shown above, a small proportion of 1-year fish is taken in the Macquarie, but not in either of the other rivers.

Statistical analysis shows a significant correlation between the catches by anglers and the survivors from stocking in the Meander River in 1950–51 and the two

following seasons, and in the Macquarie River in 1952–53: the rest show no significant correlation. This does not necessarily mean that in these cases anglers' catches were dependent on fish released: it could be merely that the rate of stocking had been such as to resemble the composition of the normal populations which, as has been shown, are similar within each river throughout. If anglers' catches had depended on released

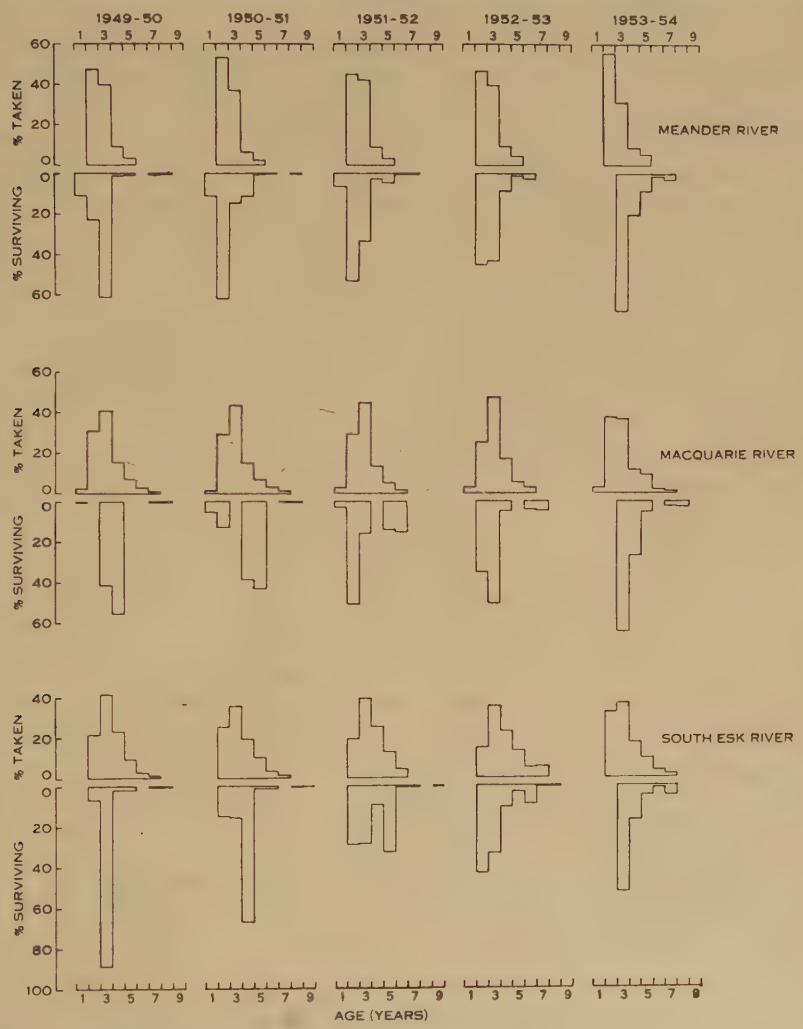

Fig. 5.—Percentage age distribution histograms of fish taken by anglers (above) and takable survivors from stocking (below), during five seasons in the Meander, Macquarie, and South Esk Rivers.

fish there should have been a significant correlation in every case, which was clearly not so. The most striking discrepancy was in 1953–54, in which there were no 2-year fish available from stocking because no yearlings were released in this system between July 1952 and June 1953, and no fry were released there in the previous season, yet the bulk of the fish taken by anglers were 2 years of age. It seems clear that anglers' catches

do not reflect the number of fish released from hatcheries and there is little support for any claim that the fishery is dependent on such releases. The 2-year fish caught in 1953–54, representing 45 per cent. of all fish taken by anglers, must have been survivors of natural spawning. It will be remembered, too, that this season showed an improvement in both daily catch and annual catch per angler over the preceding season.

It was pointed out in Section II(*b*)(ii) that the increase in the mean length of fish in the South Esk from 1949–50 to 1952–53, which was followed by a sudden fall in the next season, could have been due to a steady reduction of the population followed by heavy restocking. This would imply that there was a decrease in the porportion of 2-year fish in the catches up to 1952–53, followed by an influx of fish of this age in 1953–54. Figure 5 shows that this is what happened, and explains the rise and subsequent fall in the mean length of fish, but it also shows that there were no 2-year fish available from stocking in this season; the only survivors from stocking were 3 years and older. This indicates that the 2-year fish which represented 32 per cent. of anglers' catches from this river in that season must have been the result of a successful natural spawning in 1951. It was also shown (Fig. 2) that in the Macquarie there was an influx of small fish (10–11 in.) in 1951–52, which suggested successful spawning in 1949. Scales readings show that such fish would have been 2+, and Figure 5 shows that there was an increase in the proportion of 2-year fish available from stocking, but this apparently had little effect on the catch, which retained the same general composition as in previous years.

III. The North Esk River System

(*a*) *Environmental Characteristics*

The North Esk River rises on the slopes of Ben Nevis (3900 ft) and flows southwards for about 10 miles to a point at which it receives the Ford River, a tributary of similar size rising on Legge's Tor (5160 ft) and draining the northern end of the Ben Lomond Range, and Rose's Tier. From the confluence the general direction of flow is westerly for a distance of 16 miles, during which it receives five minor tributaries, two from the south and three from the north. It then turns north-westerly to discharge into the Tamar estuary at Launceston. Its one major tributary, the St. Patrick's River, rises in streams draining the country to the north of Ben Nevis, and after flowing somewhat north of west for about 12 miles it turns south-west and later south to flow into the North Esk about 20 miles from Launceston. It receives several small tributaries: five from the south and one from the north.

The two rivers are very similar, consisting of tumbling stretches interspersed with occasional pools, in general with a fairly steep gradient, though there are places where the river floods during heavy winter rains. The gradient over the first 10 miles from the mouth is about 2 per mille, and the width is 25 m or more; this places it in the grayling zone as defined by Huet (1954); over the next 30 miles the mean gradient is about 6 per mille, and the width is greater than 18 m, which places it wholly in the trout zone. Above it is entirely of gradient and width appropriate to the trout zone. Grayling do not occur here, neither is their place taken by other species, and trout occupy the entire length of the river. The middle and upper reaches receive 40–60 in. of rainfall per annum, and measurements of water flow in the middle reaches of the North Esk made over the past 28 years indicate a mean monthly flow of 183 cu. ft/sec

(range, 20 to 1066). As far as is known there are no falls in this system which could act as a barrier to the upstream migration of fish, though there are several stretches of rapids.

(*b*) *Results and Discussion*

(i) *The Daily Catch.*—Returns from an average of 12 anglers per season yield the figures for mean daily catch per angler given in Table 8. These indicate a downward trend which statistical analysis has shown to be quite significant for the two rivers separately and for the system as a whole.

(ii) *Fish Lengths.*—The results of fish measurements provided by anglers are given in Table 9. The differences between the means within each river are statistically quite significant. While the upward trend in the St. Patrick's reached a maximum in 1951–52 and was followed by a decrease in the two succeeding seasons, in the North

TABLE 8

MEAN DAILY CATCH PER ANGLER FROM NORTH ESK RIVER SYSTEM

Season	Number of Anglers	Number of Fish	Number of Days	Fish per Day
1945–46	8	172	46	3·7
1946–47	17	592	93	6·4
1947–48	14	701	100	7·0
1948–49	2	7	4	1·8
1949–50	19	511	122	4·2
1950–51	16	262	66	4·0
1951–52	12	296	86	3·4
1952–53	15	149	75	2·0
1953–54	9	42	20	2·1

Esk there has been an upward trend from 1950–51 onwards, which could indicate a decrease in the population. It is doubtful if this is so since the last three seasons were marked by the inclusion of fish of 24 in. and over, not recorded for previous seasons, and when these are excluded the means for these seasons are 12·6, 12·6, and 12·7 in. respectively, but the differences are still quite significant statistically.

(iii) *Growth and Age.*—Scale samples were taken from 162 fish caught in the upper reaches of the North Esk, and from 21 fish taken in the St. Patrick's during the 1949–50 season. The mean lengths of fish at each year of age are shown in Figure 6, from which it would appear that fish from the St. Patrick's are consistently smaller than those from the North Esk. The difference is statistically significant and the two groups cannot be pooled. Statistically, the differences between age groups within the North Esk are also significant. Growth data for this system are rather inadequate, but the results of the study of a large series of scales taken from fish in both streams in connexion with a population survey carried out by electro-fishing will be presented in a later paper.

(iv) *Condition.*—The mean value for the condition factor of fish in the North Esk (1·38) is very high. The usual downward trend with increasing age was found, though

it was not as marked as in the rivers of the South Esk System. Insufficient reliable data were available for fish from the St. Patrick's.

(v) *Mortality Rates.*—Using the method already described, mortality rates have been calculated for the North Esk. There are insufficient data for similar estimates for

TABLE 9

MEAN LENGTHS OF FISH FROM NORTH ESK AND ST. PATRICK'S RIVERS

Season	North Esk River		St. Patrick's River	
	Number of Fish	Mean Length (in.)	Number of Fish	Mean Length (in.)
1949–50	285	12·0	69	10·7
1950–51	113	11·1	132	10·5
1951–52	120	12·8	65	11·3
1952–53	179	12·8	28	10·5
1953–54	37	13·0	25	10·3
1949–50 to 1953–54	734	12·2	319	10·7

the St. Patrick's and the significant differences in mean lengths at capture make it impossible to pool the data, or to apply North Esk rates to the St. Patrick's. The results for the North Esk are shown in Figure 7. The proportion of takable fish in

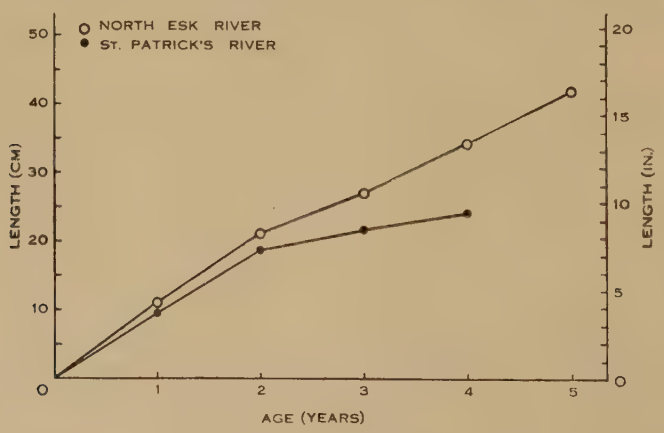

Fig. 6.—The growth of fish in the North Esk and St. Patrick's Rivers.

relation to the estimated total available shows that only 7 per cent. of 2-year and less than 1 per cent. of 1-year fish are likely to be taken. The low value for 2-year fish, compared with that of other rivers, is due to the smaller size of fish in this stream. The approximate annual mortality in this stream is 70 per cent.

(vi) *Annual Catch per Angler.*—Data for the mean annual catch per angler are given in Table 10 for each river and for the system. Statistical analysis shows that the differences between the means for the North Esk system are significant only at the 5 per cent. level. Examination of the returns shows that the high values for the early years were influenced by the returns of a few highly successful anglers who ceased to submit returns in later years, but even when the catches made by these anglers are omitted the differences are still significant at the same level. There must, however,

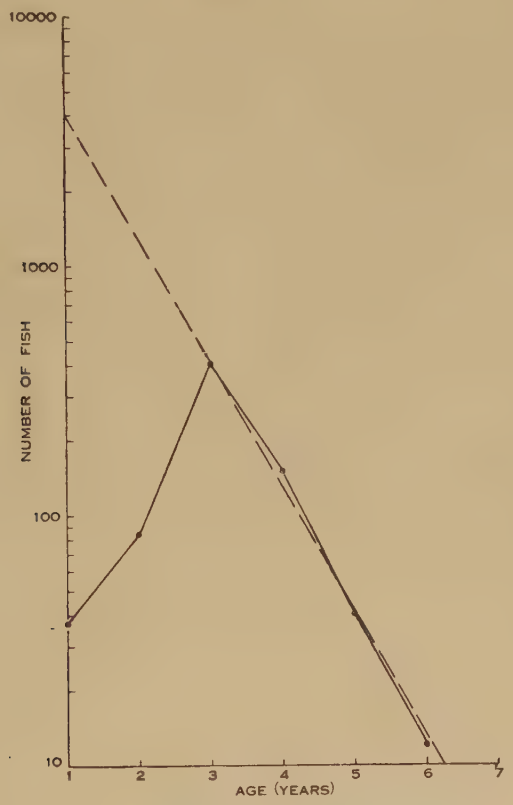

Fig. 7.—Catch curve for the North Esk River.

remain some hesitancy in accepting the fall shown by the figures as representing the true state of affairs in this system. Again there is a close relationship between the mean annual catch per angler and mean number of days spent fishing by each angler. The correlation coefficient is quite significant for the North Esk system, and when the two components are treated separately it is found to be quite significant for the St. Patrick's River, and significant at the 2 per cent. level for the North Esk.

(vii) *Estimated Total Catch.*—A corrected estimate of the number of licenced anglers who fished in the North Esk system for each season was given in Table 4. Using these figures, together with the mean annual catch per angler, total annual catches have been estimated for the system, and the values are given in Table 11 together with the coefficient of variation and standard error. No great reliance can be

placed on these values; the coefficient of variation shows a considerable range, due to various causes. It is most unlikely that 1948–49 was really as poor a season as the

TABLE 10

MEAN ANNUAL CATCH PER ANGLER FROM NORTH ESK RIVER SYSTEM

Season	North Esk River			St. Patrick's River			North Esk System		
	Number of Fish	Number of Anglers	Fish per Angler	Number of Fish	Number of Anglers	Fish per Angler	Number of Fish	Number of Anglers	Fish per Angler
1945–46	224	8	28·0	146	7	20·9	370	9	41·1
1946–47	265	13	20·4	460	11	41·8	725	18	40·3
1947–48	753	12	62·8	492	11	44·7	1245	17	73·2
1948–49	11	3	3·7	1	1	1·0	12	3	4·0
1949–50	410	21	19·5	192	10	19·2	602	23	26·2
1950–51	134	14	9·6	132	10	13·2	266	16	16·6
1951–52	127	11	11·5	183	5	36·6	310	14	22·1
1952–53	100	12	8·3	23	6	3·8	123	15	8·2
1953–54	18	8	2·3	31	6	5·2	49	9	5·4

figures indicate; the estimated total catch for this season is based on the returns of only three anglers, who took 7, 3, and 2 fish respectively. The number of anglers making returns may have a considerable influence on the estimated totals.

TABLE 11

ESTIMATED TOTAL CATCHES FROM THE NORTH ESK RIVER SYSTEM

Season	Number of Anglers	Mean Number of Fish per Angler	Estimated Total Catch*	Coefficient of Variation	Standard Error*
1945–46	563	41·1	23,000	0·438	10,000
1946–47	860	40·3	34,500	0·339	11,500
1947–48	811	73·2	59,500	0·382	22,500
1948–49	543	4·0	2,200	0·663	1,500
1949–50	1161	26·2	30,500	0·376	11,500
1950–51	1085	16·6	18,000	0·315	5,700
1951–52	1620	22·1	36,000	0·751	27,000
1952–53	1328	8·2	11,000	0·354	3,900
1953–54	1071	5·4	5,800	0·515	3,000

*Values above 10,000 are adjusted to the nearest 500, and below to the nearest 100.

Allen and Cunningham (1957) found an upward bias in the estimate of catch associated with a reduction in the number of returns. While it is doubtful if the number of anglers making returns contributes any consistent bias, it is clear that as

the returns become fewer, any bias that they have will become of increasing importance. This is shown by the two cases quoted here, where for different reasons bias may have influenced the results.

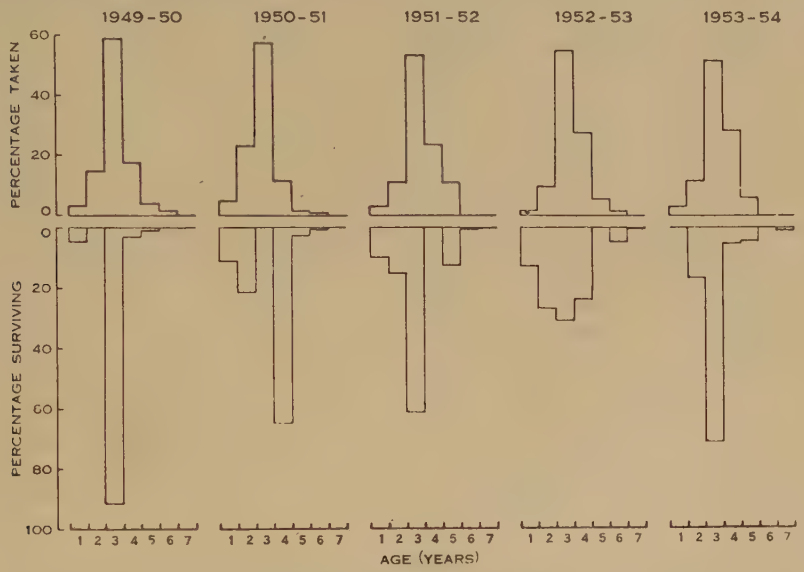

Fig. 8.—Percentage age distribution histograms of fish taken by anglers (above) and takable survivors from stocking (below), during five seasons in the North Esk River.

(viii) *Summary.*—The daily catch per angler shows a statistically significant downward trend. A slight increase in the mean length of fish taken by anglers is

TABLE 12

TAKABLE SURVIVORS FROM STOCKING IN RELATION TO TOTAL CATCH FROM NORTH ESK RIVER

Data	Season				
	1949–50	1950–51	1951–52	1952–53	1953–54
Takable survivors	846	363	552	423	683
Total catch	20,700	9,100	14,600	9,800	2,200
Ratio	1:24·5	1:25·1	1:26·4	1:23·2	1:3·2

evident, and is statistically significant. The growth rate is very similar to that found in the South Esk River, and the condition factor is also quite high. The approximate annual mortality rate is around 70 per cent. Estimates of annual catch per angler and of total catch are of doubtful accuracy owing to insufficient data, but the catch per angler can be correlated with the number of days spent fishing.

(c) *The Relationship between Total Catch and Survivors from Stocking*

Because of uncertainty as to the mortality rate in the St. Patrick's River it has been possible to relate estimated total catches to the probable numbers surviving from stocking in the North Esk River only. Table 12 shows that for the last five seasons the mean ratio was 1 : 20, and calculations for the preceding four seasons yield a mean ratio of about 1 :100. Stocking in this system was much heavier towards the end of the 9-year period. Ignoring the figures for 1953–54, for which the estimated total catch has little value owing to the few returns on which it is based, the maximum possible contribution made by hatchery-reared fish is between 4 and 5 per cent. of the estimated total catch compared with about 10 per cent. in the South Esk system.

The percentage age distribution of the fish taken by anglers and of the takable survivors from stocking are shown in Figure 8. Although relatively few fish were recorded from the North Esk during 1953–54, when these are allocated to their age groups they present a picture which very closely resembles those for the other seasons, which suggests that they were representative of the population. It is clear that anglers' catches show the same picture from season to season (although statistical analysis shows a quite significant difference between seasons for anglers' catches and a very significant difference for survivors from stocking) and that the main fishery is on the 3-year and older fish. There is no clear relationship between anglers' catches and survivors from stocking. Statistical analysis shows a significant correlation between the two for 1949–50 and 1953–54 only.

IV. Conclusions

It would seem that there has been a general fall in the daily catch per angler throughout this area, except in the Meander River; in the remaining rivers this fall becomes progressively more marked and of increasing statistical significance from west to east within the basins of the South and North Esk Rivers. Comparison between the fall in daily and annual catch per angler and the increase in the number of licences issued shows a clear correlation. In order to show this more clearly the data from the North and South Esk Rivers may be combined. This is justified because with the majority of anglers from this district being resident in Launceston, and both rivers being equally accessible, it is natural that some anglers should fish both rivers. The figures show that 21 per cent. of anglers making returns during the nine seasons fished both rivers.

The combined data, together with the total number of licences issued (Table 4), are plotted in Figure 9. This shows that the daily catch and annual catch per angler follow almost parallel courses, with very similar downward trends; at the same time the number of licences issued shows an equally clear upward trend. The negative correlation between number of licences and daily catch over the nine seasons is reasonably good (significant between the 5 and 2 per cent. levels), and that between number of licences and annual catch is very good (significant at 1 per cent. level). There can be little escape from the conclusion that the increase in licences has been accompanied by a fall in both catching rate and annual catch.

At first sight this would lead to the conclusion that the more anglers there are the fewer fish there will be for each angler, or that these streams are being fished to their full capacity, or even overfished. If this were so, it would follow that as fast as fish

attained the minimum legal length they would tend to be removed from the population, and this would have two effects: (1) there would be few, if any, large fish, which would have appeared in decreasing proportions over the period; (2) because of the removal of large fish the average length would fall to something a little over the minimum legal length. These in turn would result in less competition for food with a consequent improved growth rate over the seasons.

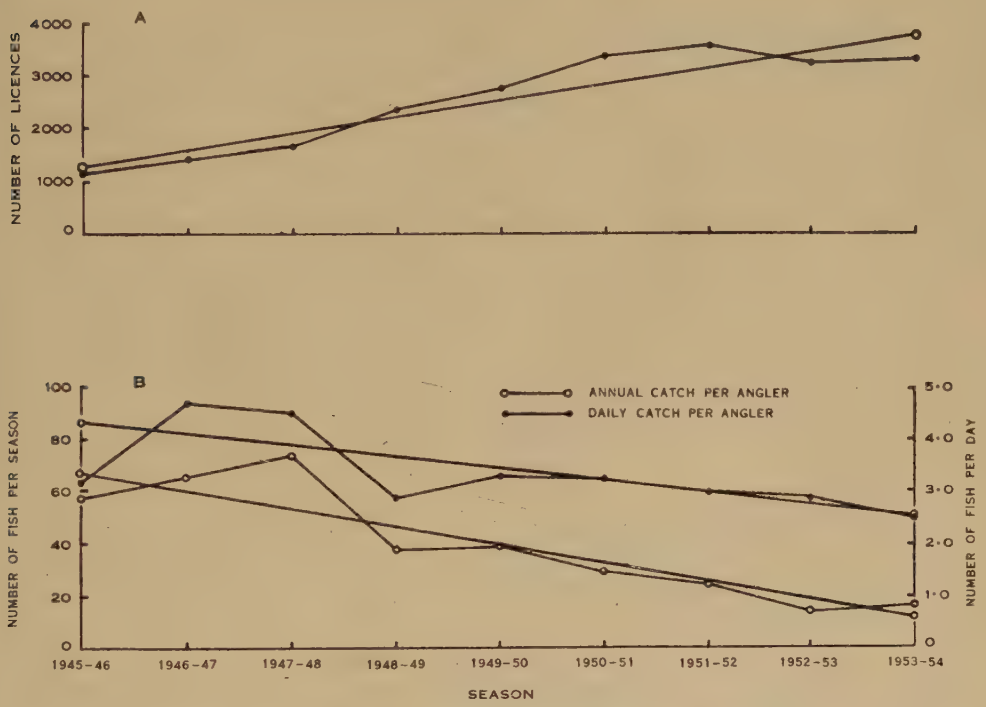

Fig. 9.—*A*, number of licences, and *B*, annual and daily catch per angler, from the North and South Esk Rivers combined, during nine seasons. The regression lines indicate the direction of the trends.

It has been shown (Section II(*b*)(ii)) that in the South Esk system there has been no tendency over the last five seasons for the average length at capture to approach the minimum legal length of 9 in., either for individual rivers or for the system as a whole, and similarly for the North Esk (Section III(*b*)(ii)), in which any change has been in the other direction owing, it may be noted, to the appearance of large fish in later seasons which had not been recorded earlier. It has also been shown, in Figures 5 and 8, that there has been little or no change in the representation of the different age groups in anglers' catches from any of these rivers. Moreover, where scale samples were available for two seasons no significant differences were found. All the available evidence, therefore, points to no change in the fish populations over this period and discounts any possibility of overfishing being responsible for the fall in catching rate.

Since this fall undeniably exists in the analysis of the returns, the most obvious explanation is that put forward earlier (Nicholls 1958), that the returns have come

largely from a new set of anglers each year, many of whom were probably fishing for their first season and lacked experience in the art of angling. Of those anglers who fished in the South Esk system from 1949–50 onwards it is found that each year about 60 per cent. of the returns came from anglers who had not made returns in earlier years. This raises again the question of the reliability of the returns and whether they are truly representative. It has been pointed out that the majority of those who submitted returns prior to 1949–50 have not done so since. In this season there was a change in the form of return required, which may have influenced the results. If the data for the nine seasons in the South Esk system are separated into two parts it is found that the mean daily catch per angler from 1945–46 to 1948–49 was 3·5 fish, and from 1949–50 to 1953–54 it was 2·8. Statistical analysis shows no significant difference between the means for the seasons within each period, which suggests that there was a real difference in the samples of anglers making returns in each period. Within the North Esk system it is found that the mean daily catch up to 1948–49 was 6·1 fish and for the next five seasons it was 3·4; again statistical analysis shows no significant difference for the first four seasons, but for the last five it was quite significant. Doubts on the reliability of returns are supported by the data quoted for anglers in the Deloraine district who had not submitted returns (Section II(*b*)(viii)). This question has a wider application, in particular to the data presented for the North-West Region (Nicholls 1958), and the matter will be reviewed in a later paper.

V. Acknowledgments

In addition to the acknowledgment of the assistance received from official sources, thanks are also due to those anglers who sent in returns of their catches, and especially to those who cooperated by carefully recording their catches, together with scale samples, from the rivers of this district.

I am greatly indebted to Mr. J. M. Wallace of Launceston for making available his diary of fishing in these rivers since 1941, and for permitting me to publish the results of the analysis; also to Mr. L. D. Cameron and Mr. F. T. Butler of Deloraine for carrying out the personal canvasses of anglers in that district in two seasons. The information thus provided has been of great value.

Mr. P. Sprent has again assisted with advice on the statistical treatment of results, and the final form of the text owes much to the helpful comments of Mr. K. R. Allen. To all these my thanks are offered.

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REPRODUCTION IN AUSTRALIAN PEARL OYSTERS (LAMELLIBRANCHIA)

III. PINCTADA ALBINA (LAMARCK): BREEDING SEASON AND SEXUALITY

By D. J. Tranter*

[*Manuscript received October* 21, 1957]

Summary

Pinctada albina breeds continuously throughout the year, but most actively during April and May when sea temperatures begin to fall. Thus the species resembles the majority of tropical marine invertebrates in the former respect but differs from them in the latter. The heaviest spatfalls occur from June to August when sea temperatures are at a minimum.

This species is hermaphrodite, with a general tendency toward protandry. Both male-female and female-male sex changes, and the bisexual condition which sometimes prevails during change-over, have been observed. Sex change in bivalves is discussed, and it is suggested that the phenomenon can best be explained in terms of a weak hereditary sex-determining mechanism, and germ cell rudiments responsive to the food reserve level in the body such that male differentiation is favoured at lower levels and female differentiation at higher levels.

I. Introduction

It has already been shown (Tranter 1958*a*) that *Pinctada albina* reaches sexual maturity at a very early age, and the manner in which the primary gonad is laid down has been outlined. The developing germ cells were described in a second paper (Tranter 1958*b*). It now remains to be shown whether there is periodicity of gonad development in the adult; the problem is resolved in this paper. In addition, two unusual features briefly mentioned in the earlier papers are discussed more fully in the light of further data. They are: (i) that most young oysters are male; (ii) that occasionally both male and female germ cells may occur in the same gonad.

Since ripe gonads and recently settled spat may be seen at any time, the breeding season investigations have been concerned primarily with relative breeding intensities. The term "major breeding season" is understood here to mean the period when the majority of individuals liberate the most gametes; this is preceded by a period of widespread gonad development and followed (under normal circumstances) by a period of heavy spat settlement.

Natural spawning of *P. albina* is not readily visible and it is difficult to assess directly the concentration of gametes in the sea. It is possible, however, by regular sampling of the population, to determine whether (and if so, when) there is a sudden sustained decrease in the percentage of ripe gonads; this may be interpreted as a major spawning. Such evidence may be augmented by regular observations on spat settlement density. It is not possible to compare the concentration densities of larvae at different times since these form an inconspicuous part of the plankton and cannot as yet be distinguished from the larvae of allied pearl oyster species.

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Just as the major breeding season of *P. albina* is not readily apparent from random observations on gonad condition, so does the apparent sex-separateness of this species hide the true nature of its sexuality. For, although smears from the gonad almost invariably show gametes of one sex only, the fact previously noted (Tranter 1958*a*) that the great majority of young oysters mature as males suggests that the species may be protandric. This conclusion can be tested by making consecutive records of the sex of individual oysters over a period of time, or by studying gonad sections which may show a degree of bisexuality not apparent in gonad smears.

II. Materials and Methods

The methods of investigation are detailed below. Except where otherwise indicated, the samples were taken from the Thursday I. area.

(*a*) Microscopical studies of stained gonad sections (histological techniques as in papers I and II (Tranter 1958*a*, 1958*b*)).

(1) Regular samples from a selected group of oysters, of common origin and similar age.
Preliminary series: August 1953–May 1954; fortnightly intervals; sample size, 5; total number examined, 80.
Main series: March 1954–February 1955; fortnightly intervals; sample size, 20; total number examined, 500.

(2) Arbitrarily selected samples from the parent population: total number examined, 120.

(*b*) Periodic observations on the gonad conditions of regular samples from the parent population.—1953–55; fortnightly intervals; sample size, 25; total number examined, 1900.

(*c*) Occasional observations on the gonad condition of miscellaneous samples.

(1) Samples of young oysters from various areas during the period of most widespread gonad development: sample size, variable; number examined: Thursday I. 1953–55, 781; Moreton Bay 1955, 347.

(2) Miscellaneous samples from the adult population at Thursday I.: 1952–56; sample size, variable; total number examined, 627.

(3) Miscellaneous samples from the adult population at areas other than Thursday I.: 1952–55; sample size, variable; total number examined, 1951.

(*d*) Consecutive observations on the sex and gonad condition of particular oysters.—The gonad was observed by wedging open the valves and smoothing away the gill lamellae to expose the gonad area of the gut loop and base of the foot. The wedged oysters were held left valve uppermost with the open shell edge toward the observer, and were illuminated by light falling over the observer's left shoulder. Sex could usually be determined from gonad colour alone, but gonads were incised and smears taken for further observation. Oysters placed in running water often opened readily and could be wedged directly; others had to be opened forcibly with a special speculum-like instrument. Care was taken in all cases not to overstrain the adductor muscle by opening the valves too far; nevertheless, handling in one way or another

caused a mortality of approximately 10 per cent. In all, 256 observations were made, on 91 oysters, examination being at 4-monthly intervals.

(*e*) Observations on spatting.

(1) Length frequency distributions. The entire catch was removed from the following collectors and measured: hull of M.V. *Reliance* exposed for a period of 15 months, catch consisting of 580 specimens taken October 5, 1953; Possession I. spat collector (I) exposed for a period of 4 months, catch consisting of 428 specimens taken March 10, 1956; Possession I. spat collector (II) exposed for a period of 8½ months, catch consisting of 359 specimens taken August 4, 1956. The data were arranged as frequency distributions and the peaks regarded as peaks of spatting intensity.

(2) Spat-plate data. A collector designed by Mr. J. S. Hynd, was hung from a raft near Possession I. about 1 fathom beneath the surface (for map, see Tranter 1958*a*). It consisted of five pairs of fibrolite plates housed in an iron frame, and periodically (usually every 3 months) the plates were changed, the frame scraped, and the catch counted.

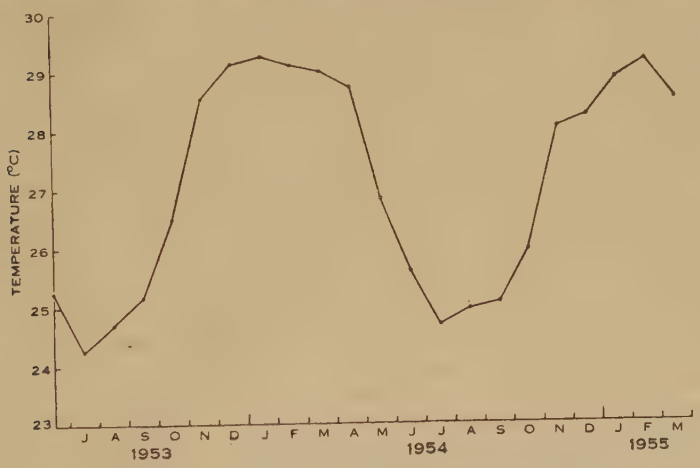

Fig. 1.—Mean monthly sea temperatures at Thursday I.

III. Breeding Season

(*a*) *Seasonal Sea Temperatures at Thursday Island*

The mean monthly sea temperatures at Thursday I. from June 1953 to March 1955 are plotted in Figure 1. The annual range is approximately 5°C. The coldest month is July, and the warmest January or February. For the purposes of this discussion these may be regarded as midwinter and midsummer respectively. The most rapid temperature rise takes place between September and November, and the most rapid decrease between April and June.

(*b*) *Histological Investigations*

It was shown previously (Tranter 1958*b*) that the gametogenic cycle of *P. albina* consists of two principal phases which were termed "development" and "regression",

TABLE I

HISTOLOGICAL CLASSIFICATION OF GONAD STATE OF REGULAR FORTNIGHTLY SAMPLES

The "Activity Index" permits comparison between the various samples; to obtain this index, the subscripts 1–5 of stages d_1–d_5 (gonad development) and 1–3 of stages r_1–r_3 (gonad regression) are taken as units of development and regression respectively; for each sample, the individual subscripts are summed and expressed as percentages of the maximum totals, which are as follows: d, $5 \times 20 = 100$; r, $3 \times 20 = 60$; $i = 20$.

Date	Sample Size	Histological Diagnosis of Individual Gonad Activity										Activity Index of Sample (%)*		
		Inactive	Pure Phase								Overlapping Phases				
			d_1	d_2	d_3	d_4	d_5	r_1	r_2	r_3	Unisexual	Bisexual	Inactivity	Development	Regression
2.iii.54	20					7	12	1					0	88	2
29.iii.54	20					3	1	3	4	9			0	17	63
14.iv.54	20					15	4	1					0	80	2
30.iv.54	20				1	8	4	5	1		Fd_5r_1†		0	60	13
11.v.54	20				2	2		6	5	4	d_1Fr_3‡		0	15	52
25.v.54	20					1	2	6	6	5			0	14	55
8.vi.54	20	6	1		1		2	4	2	4			30	14	33
21.vi.54	17	6				1	3		2	2	Md_1r_2; Md_1r_3	Fd_1Mr_2	35	26	33
5.vii.54	20	8		2	3	1			3	3			40	17	25
20.vii.54	20	7	4		5	1				2	Md_1r_3		35	24	15
3.viii.54	20	7	1	3	3	2				3	Md_1r_2		35	25	18
16.viii.54	20	8	2		2	7		1					40	36	2
30.viii.54	19	6	5		3	3					Fd_1r_2; Md_2r_3		30	30	8
13.ix.54	20	7			2	8	2				Md_2r_1		35	50	2
27.ix.54	19	2	1		3	10	3						10	68	0
11.x.54	20	5	1			9		2	1			Fd_1Mr_2; Fd_1Mr_1	25	39	12
25.x.54	19		1	1	13		1	3					0	49	5
8.xi.54	19	2	1		7	6	2	1					10	56	2
22.xi.54	20				2	18							0	78	0
6.xii.54	20	1		1	1	15					Md_2r_1	Fd_2Mr_2	5	69	5
20.xii.54	19				2	13	2		1		Fd_1r_3		0	73	10
4.i.55	20		1		8	9						Fd_1Mr_1; Fd_2Mr_1	0	64	3
17.i.55	20	2			9	7		1				Fd_2Mr_1	10	57	3
7.ii.55	20				1	16	1	1		1			0	72	7
21.ii.55	19	1			8	6	2		1			Fd_1Mr_1	5	62	5

*Corrected values based on a sample size of 20. †Localized areas of spawning. ‡Sex of developmental phase difficult to determine.

and that the latter is the result of two processes—spawning, and gonad resorption. Nine basic histological stages of gonad activity were recognized. These are: d_1–d_5, development; r_1–r_3, regression; i, inactivity. However, since the phases of development and regression often overlap, additional combinations of stages were often found.

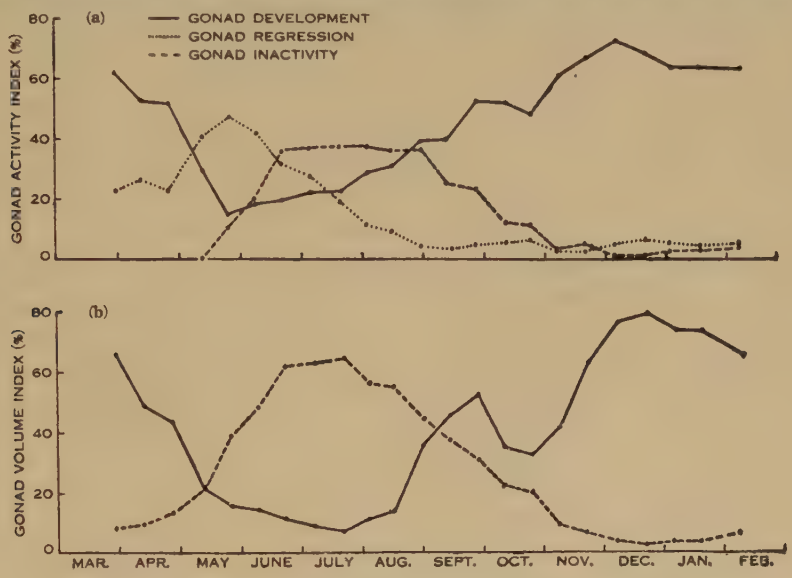

Fig. 2.—(*a*) Seasonal cycle of gonad activity as indicated by the gonad histology of oyster samples taken at fortnightly intervals from March 1954 to February 1955. The plotted values for each fortnight represent the extent of development, regression, and inactivity of the gonad relative to a maximal value (100 per cent.) for each of the three phases. (*b*) Seasonal cycle of gonad development as indicated by the macroscopic gonad appearance of the same series of samples. Regressing gonads are grouped with developing ones to yield an overall "gonad volume index" for each sample; each plotted value along the development curve represents the volume occupied by the gonads of the sample relative to that when all gonads are full (100 per cent.). The plotted values along the inactivity curve are the percentage frequencies of empty gonads. All curves have been smoothed using a moving average of three.

Regular samples of oysters have been classified in this way (Table 1) and the data used to show the relationship of the gametogenic cycle to the seasons of the year.

In estimating the general level of gonad development and gonad regression in a sample, the subscripts n of the gonad stages d_n or r_n of each individual are treated as units, and their sum Σn taken. The values obtained are corrected where necessary on the basis of a sample size of 20. The corrected values are expressed as percentages of a maximal value, which is for gonad development (d), $5 \times 20 = 100$; for gonad regression (r), $3 \times 20 = 60$; and for gonad inactivity (i), 20. Thus the degrees of development, regression, and inactivity may be compared within each sample and between the various samples. The curves in Figure 2(a) are derived from these values. To reduce sampling error, the curves have been smoothed by the moving

average method, such that the plotted percentage value at each point of time is the mean of three consecutive values centred at that point.

Figure 2(*a*) shows gonad development to be at a minimum in late May following a major spawning; at this time gonad regression has reached its peak and a few inactive gonads are beginning to appear. During the colder months of June and July,

TABLE 2

GONAD CLASSIFICATION OF REGULAR FORTNIGHTLY SAMPLES

Date	1953				Date	1954				Date	1955			
	Gonad Stage					Gonad Stage					Gonad Stage			
	3	2	1	0		3	2	1	0		3	2	1	0
Jan. 12	25	0	0	0	Jan. 6	22	3	0	0	Jan. 4	23	2	0	0
Jan. 26	24	1	0	0	Jan. 22	20	1	1	3	Jan. 17	19	3	0	0
Feb. 9	21	1	2	1	Feb. 4	23	2	0	0	Feb. 7	20	4	0	1
Feb. 23	21	3	1	0	Feb. 19	21	4	0	0	Feb. 21	8	8	5	4
Mar. 9	25	0	0	0	Mar. 2	24	1	0	0	Mar. 8	17	4	1	3
Mar. 23	25	0	0	0	Mar. 18	15	5	3	2	Mar. 23	17	4	1	3
Apr. 8	24	1	0	0	Mar. 30	4	4	9	8	Apr. 5	25	0	0	0
Apr. 22	21	3	1	0	Apr. 14	23	2	0	0	Apr. 18	22	1	2	0
May 5	21	3	0	1	Apr. 30	4	9	12	0	May 4	23	1	0	1
May 19	0	14	11	0	May 11	0	0	21	4	May 17	13	10	2	0
June 3	4	9	12	0	May 25	5	9	5	6	June 1	15	10	0	0
June 15	8	9	8	0	June 8	0	6	4	15	June 17	8	7	4	6
June 29	2	4	10	9	June 21	5	1	11	8	July 4	1	9	9	6
July 15	9	4	3	9	July 5	5	4	4	12	July 19	2	4	19	0
July 23	8	8	6	3	July 20	2	7	9	7	July 29	4	4	10	7
Aug. 13	6	6	9	4	Aug. 3	7	5	5	8	Aug. 19	9	7	2	7
Aug. 26	0	6	15	4	Aug. 16	0	4	10	11	Aug. 29	8	3	11	3
Sept. 16	18	3	4	0	Aug. 30	0	0	7	18	Sept. 9	8	6	3	8
Sept. 30	11	9	4	1	Sept. 13	0	0	8	17	Sept. 23	9	13	1	2
Oct. 14	18	4	2	1	Sept. 27	2	10	3	10	Oct. 10	16	7	2	0
Oct. 29	6	6	4	8	Oct. 11	0	5	18	2	Oct. 24	18	4	2	1
Nov. 12	5	13	4	3	Oct. 25	5	9	9	2					
Nov. 25	22	2	1	0	Nov. 8	1	6	15	3	Nov. 21	14	7	4	0
Dec. 11	23	1	1	0	Nov. 22	22	2	0	1	Dec. 7	4	15	4	2
Dec. 21	8	13	4	0	Dec. 6	11	12	2	0	Dec. 15	17	7	1	0
					Dec. 20	17	5	2	1	Dec. 23	21	4	0	0

unspent gonad material is resorbed and the frequency of inactive gonads reaches a maximum which is maintained till August. During this month these resting gonads begin to redevelop. Other gonads gradually recover after the major spawning without passing through an inactive phase. A developmental maximum is reached in December, and this is maintained (at a slightly lower level) during the warmer months. In April the degree of gonad development falls rapidly as the population spawns; by

the end of May this is complete. There is a lesser developmental maximum in late September which precedes a possible minor spawning.

The histological method undoubtedly affords the most accurate means of investigating seasonal gonad activity, but it is slow and painstaking. Once the general seasonal relationship of each phase is understood, it becomes more practicable to use external gonad appearance. The feature most suited to quantitative measurement is

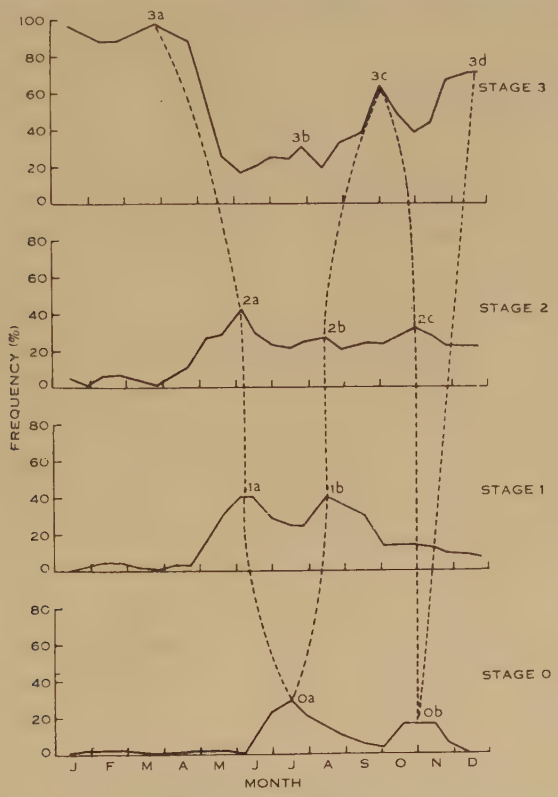

Fig. 3.—Seasonal gonad development during 1953 as shown by the variation in the percentage frequency of the selected gonad stages 3, 2, 1, and 0. The broken lines connect corresponding peaks on each of these curves to show the interrelationship between the selected stages.

relative gonad volume, that is, the extent of gonad spread relative to that in a ripe oyster. To test whether this feature is indicative of seasonal trends in gonad development, the method was applied to the same material on which the histological diagnoses were made. A percentage index was arrived at for each gonad after examining the three major gonad areas, namely, the gut loop area, the area at the base of the foot, and the stomach area. The results are plotted in Figure 2(*b*); the curves were smoothed as in Figure 2(*a*). There is a basic similarity between the two groups of results, except that, as would be expected, the earlier stages of gonad development have proved more difficult to detect by macroscopic means. It is therefore permissible to use external

gonad appearance to determine seasonal cycles of gonad development, and to adopt arbitrary stages based on relative gonad volume.

(c) *Interrelationship of the Arbitrarily Selected Stages in External Gonad Appearance*

The various stages assumed by the gonads of adult oysters during seasonal gonad development are not readily distinguishable from the corresponding stages of juvenile oysters during primary gonad development. Therefore the stages 3, 2, 1, and 0 (Tranter 1958*a*) based on relative gonad volume are used also in this study. Data for the years 1953–55 are given in Table 2.

To show the relationship between these stages, in seasonal gonad development, the data for 1953 are plotted in Figure 3. The curves have been smoothed by a moving average of three. The obvious peaks in each curve have been designated 3*a*, 3*b*, 3*c*, 3*d*; 2*a*, 2*b*, 2*c*; 1*a*, 1*b*; 0*a*, 0*b*. The broken lines relate the peaks to one another as follows.

3*a*–2*a*–1*a*–0*a*: represents the regression of the gonad which takes place during the major breeding season; since 2*a* and 1*a* are intermediate points, then the stages 2 and 1 which they represent are not only stages of development, but also stages of regression.

0*a*–1*b*–2*b*–3*c*: represents redevelopment of the gonad after the major spawning; since the peak 2*b* is not very marked, the gonad probably develops from stage 1 to stage 3 very rapidly.

3*c*–2*c*–0*b*: represents a minor spawning; the fact that the peak 2*c* is not very definite and that there is no corresponding peak along curve 1 indicates, probably, that the gonad has emptied very rapidly.

0*b*–3*d*: represents the redevelopment of the gonad after the minor spawning; the trend is not represented by peaks along curves 1 and 2 because the percentage frequencies of these stages are showing a general decrease as gonads ripen to stage 3.

Lesser peaks along these curves are of doubtful significance.

Although it is necessary to know the interrelationship of the adopted stages, curves 1 and 2, representing respectively the seasonal frequencies of gonads at stages 1 and 2, contribute little to the delineation of the general seasonal trend, and in Figure 4 (1953–1955) these have been omitted.

(d) *Seasonal Gonad Development*, 1953–1955

The three pairs of curves in Figure 4 are similar in pattern, the points of resemblance being that:

(i) The highest frequency of ripe gonads occurs during the warmer months.

(ii) The highest frequency of spent gonads occurs during the cooler months.

(iii) The most rapid decrease in gonad ripeness (spawning) coincides with the period of decreasing sea temperatures.

(iv) Lesser spawnings occur at other times of the year.

(v) Ripe gonads are present, and therefore spawning is possible throughout the year.

TABLE 3

GONAD CLASSIFICATION OF MISCELLANEOUS SAMPLES FROM THURSDAY I. AREA, 1953–1956

Origin of Sample	Date Examined	Sample Size	Percentage Frequency of Gonad Stages			
			3	2	1	0
M.V. *Pearline*	28.vii.53	13	31	31	31	7
	13.viii.53	12	58	17	8	17
	26.viii.53	12	25	33	33	9
	9.ix.53	12	58	17	8	17
	23.ix.53	10	10	50	30	10
M.V. *Reliance*	5.x.53	41	44	32	24	0
M.V. *Pearline*	7.x.53	10	60	20	10	10
	20.x.53	10	60	30	10	0
Marina rock buoy	23.x.53	18	11	67	16	6
M.V. *Pearline*	4.x.53	10	60	40	0	0
	18.xi.53	10	50	50	0	0
	2.xii.53	10	60	40	0	0
	16.xii.53	10	90	0	10	0
	30.xii.53	10	80	10	0	10
	12.i.54	10	60	20	10	10
	25.i.54	9	78	11	11	0
	10.ii.54	10	90	10	0	0
Cages, station raft	16.ii.54	25	80	12	8	0
M.V. *Pearline*	23.ii.54	10	80	20	0	0
	9.iii.54	5	40	60	0	0
	23.iii.54	5	40	20	40	0
	7.iv.54	5	20	80	0	0
	21.iv.54	5	100	0	0	0
	4.v.54	5	10	40	10	40
Quarantine wharf	5.iv.55	25	64	36	0	0
	18.iv.55	25	96	0	4	0
	4.v.55	25	56	36	4	4
	17.v.55	25	84	12	4	0
	1.vi.55	25	24	48	20	8
	17.vi.55	25	56	28	8	8
Main wharf	26.i.56	25	72	24	4	0
	7.ii.56	25	64	32	4	0
	16.iii.56	25	44	16	0	40
	10.iv.56	25	48	24	12	16
	23.iv.56	25	56	36	4	4
	3.v.56	25	88	12	0	0
	31.v.56	25	44	48	8	0
	25.vi.56	25	20	40	24	16
Total:		627				

There can be no doubt that the gonad of *P. albina* develops each year in accordance with a seasonal pattern whose main characteristics are those listed above. During the observational period, lesser spawnings occurred when sea temperatures were at a minimum (1953, 1954), at a maximum (1953, 1955), and when sea temperatures began to rise (1953, 1955). These were sometimes associated with lesser

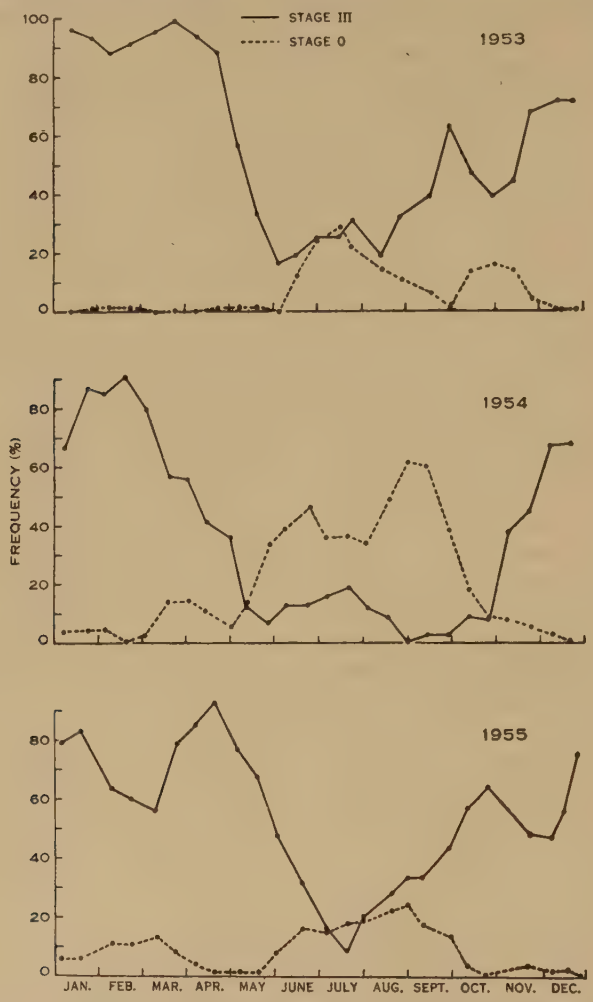

Fig. 4.—Seasonal gonad development, 1953–55, as indicated by the percentage frequency of ripe gonads (stage 3) and spent gonads (stage 0). The curves have been smoothed by a moving average of three.

maxima of spent gonads, for example, during October–November 1953, and sometimes not, for example, in November 1955. In the former case spawning was probably complete, and in the latter case only partial.

In addition to the data plotted above, observations were made on the gonad condition of a number of miscellaneous samples (Table 3). These are difficult to

TABLE 4

SEASONAL GONAD DEVELOPMENT AS INDICATED BY CONSECUTIVE EXAMINATIONS OF INDIVIDUAL GONADS

The data are arranged in a series of contingency tables in which the frequency of the various stages at the beginning of a 4-month period (columns) are associated with the frequencies at the end of that period (rows). The total number of oysters examined is designated at the bottom right hand corner of each table. Where the observations are consecutive over more than one 4-month period, the frequencies at the end of one period become the frequencies at the beginning of the next. The overall results are shown at the foot of the main table

	Frequency of Gonad Stages at Beginning of Period															
		October–January					January–May					May–September				
Frequency of Gonad Stages at End of Period	Stage	0	1	2	3	Total	0	1	2	3	Total	0	1	2	3	Total
	0	1	–	2	1	4										
	1	1	–	–	–	1										
	2	1	1	1	–	3										
	3	–	3	15	–	18										
	Total	3	4	18	1	26										
	0	–	–	1	–	1	–	1	–	9	10					
	1	–	–	2	–	2	–	–	–	5	5					
	2	–	1	–	–	1	1	–	1	3	5					
	3	6	3	16	–	25	–	1	–	8	9					
	Total	6	4	19	–	29	1	2	1	25	29					
	0	–	–	1	–	1	1	–	–	2	3	3	–	1	8	12
	1	–	–	2	–	2	–	–	–	–	–	–	–	2	2	4
	2	–	1	–	–	1	–	–	–	3	3	–	–	–	2	2
	3	2	2	9	1	14	–	2	1	9	12	–	–	–	–	–
	Total	2	3	12	1	18	1	2	1	14	18	3	–	3	12	18
	0						–	–	–	–	–					
	1						–	–	–	2	2					
	2						–	–	–	2	2					
	3						–	–	–	5	5					
	Total						–	–	–	9	9					
	0						–	–	–	–	–	–	1	1	1	3
	1						–	–	–	2	2	–	1	3	2	6
	2						–	–	–	4	4	–	–	–	–	–
	3						–	–	1	2	3	–	–	–	–	–
	Total						–	–	1	8	9	–	2	4	3	9

TABLE 4 (*Continued*)

		October	January	January	May	May	September
Overall Result	0	11	6	2	13	3	15
	1	11	5	4	9	2	10
	2	49	5	3	14	7	2
	3	2	57	56	29	15	0
	Total	73		65		27	

correlate with the general trends shown in Figure 4; however, if consideration is given to the smallness of many of the samples and to the discontinuous nature of the sampling, the data are reconcilable with those upon which Figure 4 is based. They are included here for the sake of completeness, and to show how misleading small or isolated samples can be when the species in question breeds to some extent throughout the year.

(*e*) *Consecutive Observations on the Gonad Condition of Particular Individuals*

The conclusions in the preceding sections are based on the theory that periodic observations on samples from the parent population are a consecutive record of the state of gonad development of the population as a whole. The assumption is justified so far as the general trend is concerned if the plotted curves are smoothed, for example, by using a moving average.

It has been possible, however, to keep a consecutive record of the gonad changes in a number of individual oysters. The records are subject to two limitations: (i) that the only part of the gonad which can be observed in the live oyster is the part contained in the gut loop and the base of the foot; however, this area fills and empties at approximately the same rate as the whole gonad; (ii) that at each examination, gonads were incised to give a smear; nevertheless, observations have shown that the incision heals rapidly. These limitations are therefore not serious.

The data (Table 4) show that the oysters as a whole experienced a general increase in gonad ripeness over the period October–January; a net decrease in gonad ripeness over the period January–May; and a general decrease in gonad ripeness from May to September. This evidence therefore confirms the previous conclusions (Section III(*d*)) and supports the argument by which they were reached.

(*f*) *Spatting Investigations*

Since ripe oysters are to be found throughout the year it is not unexpected to find that spat settlement is continuous. But just as there are peaks in spawning intensity, so one would expect to find peaks in spatting intensity. These may be detected in two ways: (i) by the spat-plate method; (ii) by the length frequency method.

Two pearl oyster species settled on the plates—*P. albina* and the closely related *P. fucata* (Gould). Counts were made of the numbers of each species settling within a

marked square foot of each plate over a period of time. It proved difficult to distinguish between the smallest spat of the two species, so the numbers of these were recorded jointly. The counts were made available by Mr. J. S. Hynd and are given in Table 5. From these data, estimates have been made of the *total* number of *albina* which settled during each period, and these values are also given in Table 5.

In these estimations it was assumed that, during any one period, the intensity of settlement of *albina* spat relative to that of *fucata* spat is intermediate between corresponding values for adjacent periods. Thus the ratio *albina* : *fucata* amongst the small unidentified spat of a particular period may be estimated from the counts of

TABLE 5

SEASONAL DENSITY OF SPAT SETTLEMENT AS INDICATED BY THE NUMBERS SETTING ON SPAT PLATES AT POSSESSION I.

Period of Exposure	Interval (months)	Total *Pinctada*	Unidentified (u)	Identified (i)		Estimated Total *albina*	Av. Monthly Density, *albina*	
				fucata	*albina* (a)		Identified	Estimated
13.vi.53–13.ix.53	3	363	278	11	74	276	25	92
13.ix.53–14.xii.53	3	231	84	52	95	150	32	50
14.xii.53–8.iii.54	3	9	4	0	5	7	2	2
8.iii.54–24.v.54	2½	116	56	26	34	78	14	31
24.v.54–14.viii.54	2½	942	534	74	334	782	134	313
14.viii.54–15.xii.54	4	108	3	7	98	100	25	25
15.xii.54–17.iii.55	3	234	11	142	81	85	27	28
17.iii.55–22.vi.55	3	46	9	14	23	31	8	10
22.vi.55–22.viii.55	2	762	180	30	552	711	276	355
22.viii.55–18.xi.55	3	271	57	62	152	194	51	65
18.xi.55–22.iii.56	4	123	10	22	91	99	23	25

larger (identifiable) spat of adjacent periods. The method used could be represented by the formula:

$$\text{Estimated total } albina = a_n + \frac{a_n + a_{n+1}}{i_n + i_{n+1}} \times u_n,$$

where i_n, a_n, and u_n are, respectively, the total number of identified spat, the number of *albina* amongst the identified spat, and the total number of unidentified spat, of group n, and where i_{n+1} and a_{n+1} are respectively the total number of identified spat and the number of *albina* amongst the identified spat, of group $n+1$ (see Table 5).

The actual counts and the estimated totals have been divided by the time for which the collector was exposed, to indicate the intensity of spat settlement per month. Table 5 shows the seasonal trends in spatting intensity, but the estimated values allow a more accurate comparison between the various years. The following features are apparent:

(i) Spat settlement is continuous; the lowest recorded density occurred during the period December 14, 1953, to March 8, 1954, when only five (identified) specimens settled.

(ii) Peak densities of spat settlement occurred during the periods June–August 1954, July–August 1955, and possibly also during a corresponding period in 1953.

There can be no doubt then that the height of spat settlement intensity occurs during the cooler months. This corroborates the previous evidence that the major spawning of the year takes place during the period of decreasing sea temperatures.

It was possible on several occasions to measure the entire catch from other, larger collectors. When these are exposed for a comparatively short time, that is, less than 18 months, the oysters which settle have a more or less common growth rate, and length frequency peaks may be regarded as peaks of spatting intensity. The period of exposure of the collector and the approximate growth rate of the species being known (Tranter 1958*a*), it is possible to determine approximately when these peaks of spatting intensity occurred. Such length frequency values are plotted as histograms in Figure 5.

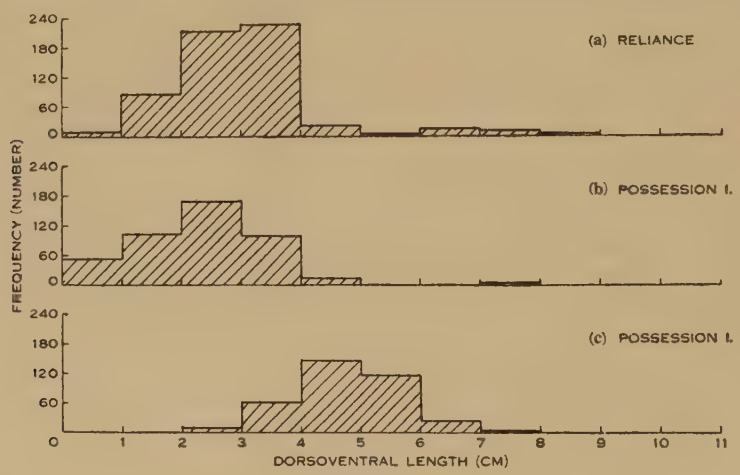

Fig. 5.—Length frequency histograms of particular catches, indicating peaks of spatting intensity: (*a*) M.V. *Reliance*, cleaned July 1952, catch examined 5.x.53; (*b*) Possession I. collector, laid 15.xi.55, examined 10.iii.56; (*c*) Possession I. collector, laid 15.xi.55, examined 4.viii.56.

The M.V. *Reliance* was a vessel moored in Thursday I. harbour, and the period of exposure represents the interval between one cleaning of the hull and the next. The Possession I. collectors were situated near the surface beneath the Possession I. raft, and were constructed of wire-netting, bondwood, and bamboo. They had been designed by Mr. J. S. Hynd to collect the spat of *P. maxima* (Jameson). The *Reliance* material, taken on October 5, ranged in size from 0 to 9 cm (dorsoventral measurement), but consisted predominantly of a group of 1–4 cm (heel depth less than 0·5 mm), less than 4 months old; these had obviously settled the previous winter. The Possession I. material from the first collector (taken on March 10) consisted of oysters whose plotted lengths approach a normal distribution (Fig. 5(*b*)). There had obviously been a substantial spat-set during the preceding months, with the heaviest concentration round about January. The catch from the second Possession I. collector

(taken on August 4) consisted in the main of oysters which settled at about the same time as on the first collector.

It is unfortunate that there are no comparable data subsequent to August 4, in which period spat settlement would be expected to be intense. Figure 4 shows that the spat-set on the Possession I. collectors originated from an early summer spawning in 1955. However, these collectors presented a vast potential attachment surface compared with that of spat plates, and the proportions of the catch do not indicate, therefore, that it was a particularly heavy spat-set; in point of fact the plates collected, over roughly the same time, only 25 *albina* per month compared with 276 (identified) the previous winter.

TABLE 6

RECORDS OF SEASONAL GONAD DEVELOPMENT OF POPULATIONS FROM AREAS OTHER THAN THURSDAY I.

Locality	Date	Sample Size	Percentage Frequency of Gonad Stages:			
			3	2	1	0
Torres Strait:						
Darnley I.	4–12.x.53	39	38	28	31	3
Mangrove I.	17.ix.54	36	11	17	19	53
Turtle I.	12.ii.53	16	100	—	—	—
Red I. Point	15.iv.53	25	84	12	—	4
Mappoon	21.xii.52	90	94	5	—	1
Groote Eylandt	23–28.vii.52	94	42	26	17	15
	3–22.viii.52	64	67	28	3	2
	5.xii.52	37	49	51	—	—
	24.xi.53	171	53	11	13	23
Moreton Bay	11.iii.55	576	37	56	5	2
	23.iv.55	803	45	42	11	2
	Total:	1951				

(*g*) *Breeding Season Outside the Thursday Island Area*

So far all the evidence has related to samples taken within the Thursday I. area (see map, Tranter 1958*a*). However, observations have been made from time to time on the gonad condition of samples from other parts of Torres Strait, Groote Eylandt (N.T.), and Moreton Bay (South Queensland). Since the samples are of various sizes, the frequency values of the gradings have been expressed as percentages (Table 6). Although in most cases the samples are of sufficient size, they lack continuity, and as a result are of only limited value in indicating the major breeding season. However, the values do not differ sufficiently from those recorded at Thursday I. at the same

time of the year to indicate that the species differs in breeding behaviour from area to area.

IV. Sexuality

(a) *Definition of Terms*

There have been many contradictory statements concerning the sexuality of bivalves, mainly because some workers have placed their own interpretation on the meaning of the terms "dioecious" and "hermaphrodite." The accepted meanings are as follows: *hermaphrodite,* containing both male and female reproductive organs (or germ cells) within the one individual; *dioecious*, containing the male reproductive organs (or germ cells) in one individual, and the female in another. Hermaphrodite and dioecious species are those in which the majority of individuals conform respectively to the hermaphrodite and dioecious patterns.

When these terms are applied to particular gonads their meaning becomes restricted and obscured, and it is better to use instead the terms "bisexual" and "unisexual"; conversely, these should not be applied to individuals or to species, where their meaning is ambiguous. In this work, the meanings of these terms are as follows: *bisexual,* containing both male and female germ cells within the gonads at a particular time; *unisexual*, containing within the gonads at a particular time germ cells of one sex only.

"Protandric" and "protogynic" refer to primary gonad maturity, such that when male gametes mature before female gametes the individual is said to be *protandric*, and when female gametes mature first the individual is said to be *protogynic*. The terms may also be applied to male–female and female–male sex changes respectively. When the terms are applied to species it is meant that the majority of individuals show that particular tendency.

(b) *The Chromosomes*

Metaphase plates are rarely seen in gonad sections of *P. albina*, and it has therefore been difficult to make chromosomal counts, or to compare the chromosomal morphologies of male and female germ cells. However, those counts which have been made do not show any significant difference between the sexes; the haploid number is approximately 10.

(c) *Protandry*

It was noted in a previous paper (Tranter 1958*a*) that the majority of young *P. albina* mature for the first time as males. This indicates that the species is protandric. To test the validity of this conclusion, observations were made during the period of maximum gonad development (November–April) on the sexual composition of a number of samples covering the entire size range of the species. (During this period, the percentage of inactive (adult) gonads is very low (see Fig. 4); consequently oysters observed with undeveloped gonad are predominantly immature.)

The data are presented in histogram form (Fig. 6), the frequencies being the percentages of neuter, male, and female oysters for each class interval of size (heel

depth). Figure 6(*a*) is based on gonad observations of 2430 specimens from Torres Strait and Groote Eylandt, and Figure 6(*b*) on 1522 specimens from Moreton Bay.

Figure 6 shows how sex ratio varies with size. Since the size dimension is proportional to age, the size range may be regarded as the lifetime of the species, and the changing sex ratio as the trend of events experienced by the average year group as it passes through life. This trend is basically similar for both groups of material, that is, there is a gradual increase in the percentage of females till late in life.

Once a year-group of a dioecious species reaches sexual maturity, there is no significant change in the sex ratio (males : females) except as the result of differential mortality, migration, or age at first maturity. In *P. albina*, there is no migration, differential or otherwise, the majority of young oysters mature in less than 6 months

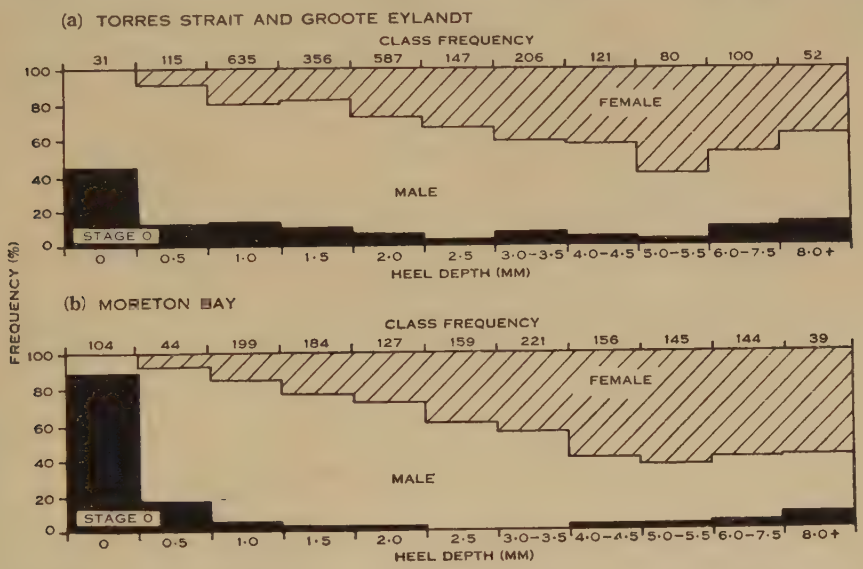

Fig. 6.—Variation with age in the percentage frequency of the sexes, illustrating the protandric sexuality of the species.

(Tranter 1958*a*), and differential mortality is unlikely—at least, early in life. The significant changes in sexual composition shown in Figure 6 are, then, almost certainly the result of sex change. The fact that there is such a close similarity between the trends of sex change in populations over 1000 miles apart suggests that this feature is of basic importance in the reproductive biology of the species. It is noteworthy that equality in the numbers of each sex is not reached until middle age.

Unless the protandric tendency is itself part of the genetic make-up of the species, the factors determining sex must be very weak in those individuals which experience sex change. The question then arises whether or not there are a minority which retain the same sex throughout life, and if so whether they are "true" (that is, genetic) males and females. The presence of such individuals in an otherwise protandric hermaphrodite species has been postulated by Orton (1927*a*), Coe (1936*a*, 1938, 1941), and Needler (1942). However, these workers failed to establish the genetic or

histological purity of the gonad; in most cases, their diagnoses were based solely on the fact that the same sexuality was retained over a period of time—a thoroughly justifiable conclusion in normal circumstances, but hardly sufficient evidence to establish purity in an individual belonging to a (predominantly) hermaphrodite species.

It seems unlikely to the author that a characteristically hermaphrodite species would contain any dioecious individuals. In the case of *P. albina* all individuals are probably potential hermaphrodites, and those which mature as females in their first year (see Fig. 6) probably pass through a prior (incipient) male phase.

(*d*) *Bisexuality of Gonads*

Table 1 shows that gonads are sometimes found containing both male and female germ cells. These do not occur in separate areas but within the same gonad follicles (Plate 1, Figs. 1, 2). Usually one sexual phase is developing and the other regressing (Plate 1, Fig. 3), but occasionally the overlapping is so great that functional gametes of both sexes are present within the same follicle (Plate 1, Fig. 4). On one occasion eggs were taken from such a gonad, and after activation they were fertilized with sperm from the same gonad; development proceeded to the morula stage.

TABLE 7

OBSERVED CHANGES OF SEX

Period Between Observations	No. of Changes	Male–Female	Female–Male
July–October 1953	1	–	1
October 1953–January 1954	4	3	1
January–May 1954	3	1	2
May–September 1954	6	2	4
October 1953–May 1954	2	1	1
October 1953–October 1954	1	–	1
Total	17	7	10

Although the examination of stained gonad sections provides direct evidence of sex change, the recorded frequency of bisexual gonads (see Table 1) is an inadequate indication of the frequency of sex change; for marked gonad bisexuality occurs only when two cycles of different sex overlap. There is possibly an equal, if not a greater, proportion of change amongst those gonads which empty completely before redeveloping, or which pass through an intermediate inactive phase.

(*e*) *Direct Evidence of Sex Change*

Between July 1953 and October 1954, consecutive observations were made on the sex of 134 oysters, consisting of 108 males and 26 females. All were initially less than 18 months old, the eldest being the females. The results are given in Table 7.

The number of observed changes was 17, or 12 per cent. of the oysters under observation. Of these, there were seven protandric changes representing 6·5 per cent.

of the original number of males, and 10 protogynic changes representing 28·5 per cent. of the total number of females. The fact that there is a reverse change is extremely important, for the trend shown in Figure 6 is, then, only the net resultant of the greater tendency toward femaleness and the lesser tendency toward maleness. Should the frequency of protogynic change approach in nature that shown to occur under experimental conditions, then the *total* frequency of protandric change must be much higher than shown in Figure 6. If this is so, then the vast majority of young males must change to females later in life, and the retention of unisexuality may be regarded as exceptional.

However, there is a general consensus of opinion that the rate of sex change in bivalves is modified by environmental conditions, good conditions favouring femaleness and bad conditions retarding it (see Section V(*b*)). This may explain the unexpectedly low frequency of protandric sex change and the unexpectedly high frequency of protogynic sex change in the experimental sample.

(*f*) *Comparison with Other Species*

(i) *Other Pearl Oysters.*—It has been shown that the sex ratio of *P. albina* tends increasingly toward femaleness as a population becomes older, and that the phenomenon can only be explained satisfactorily on the basis of extensive protandric sex change. The existence of such changes has been confirmed by direct observation. *P. albina* is therefore a protandric hermaphrodite species. The possibility that dioecious individuals exist is recognized, but considered unlikely.

With the exception of Ojima and Maeki (1955) who noted the bisexual nature of *P. martensii* gonads, other pearl oysters have always been said to be dioecious or sex-separate (Herdman and Hornell 1903, 1904, 1906; Seurat 1904*a*, 1904*b*; Allen 1906; Talavera and Faustino 1931; Galtsoff 1933, 1950; Wada 1938, 1953; Wada and Wada 1939; Craig, unpublished report, 1947; Cahn 1949; Hynd 1950; Ranson 1952; Crossland 1957). Of these workers, Herdman and Hornell recognized the possibility of sex change but concluded that their species (*P. fucata*) was "permanently dioecious"; Wada showed that *P. martensii* (= *P. fucata*) and *P. maxima* experience change of sex; Hynd agreed that in the latter species sex changes commonly occur; and Galtsoff (1950) found in a sample of 27 one specimen of *P. mazatlanica* Hanley with a bisexual gonad.

As Coe (1943) has pointed out, if sex change regularly occurs in a species, it is illogical to regard the separate sexual phases as separate individuals, and to call the species "dioecious". The individual is no less hermaphrodite because its male and female aspects are separated by a period of time, and indeed the gonad may even contain, at all times, the germ rudiments of both sexes (Tranter 1958*b*). In view of the existing evidence, it seems very likely that pearl oysters as a whole are hermaphrodite, and not dioecious as has been stated in the past.

(ii) *Other Bivalves.*—Coe (1943) pointed out that less than 4 per cent. of the described species of bivalves deviate from a strictly dioecious condition. This minority, though, contains species with every conceivable type of sexuality ranging from strict dioecism to functional hermaphroditism, and provides excellent material for studies on the essential nature of sex.

The European edible oyster (*Ostrea edulis* L.) was known to be hermaphrodite over 100 years ago, but Sparck (1925) was the first to show conclusively that the species was protandric with alternating sexual phases. His work was followed by the extensive researches of Orton (1927*a*, 1927*b*, 1933) and Cole (1942). The latter, using the histological method and oysters of known age, clearly demonstrated the pattern of sex change. His work was parallelled by that of Coe (1931, 1932*a*) and Hopkins (1937) on another larviparous species, *O. lurida* Carpentier. An early work on the American oviparous oyster *Crassostrea virginica* (Gmelin) led to the belief that all oviparous oysters are dioecious, but so many workers were able to demonstrate exceptions to this rule in later years that it soon became evident that these also were hermaphrodite, but with a lesser degree of phase overlap (Amemiya 1925, 1926, 1928, 1929—*C. angulata* (Lamarck); Amemiya 1928, 1929—*C. gigas* (Thunberg); Roughley 1928, 1929, 1933—*C. commercialis* (Iredale & Roughley); and Burkenroad 1931; Coe 1932*b*, 1938; Needler 1932; Galtsoff 1938—*C. virginica*).

Protandry dominates the sexuality of all these oysters—the antecedent germ cells of both sexes are present in the tubular ducts of the young gonads, but spermatogonia proliferate more rapidly than oogonia. After the initial male phase the sexuality tends to be dominated by the female elements, but on rare occasions the gonad may contain functional gametes of both sexes. In some instances the initial male phase is aborted, and the female phase develops directly. This succession of phases may continue season by season as in the oviparous oysters, or within each season as in the larviparous species.

Other bivalves with similar patterns of sexuality include several species of teredinids (Coe 1941) and the clam *Venus mercenaria* L. (Loosanoff 1937). In the latter species only one sex change has been found to occur, but the teredinids, for example *Teredo navalis* L. (Coe 1936*a*; Grave and Smith 1936), experience many sex changes in their short life. Pectens are usually supposed to have a bisexual gonad with distinct male and female areas, for example, *Chlamys opercularis* L., *Pecten maximus* L. (Dalmon 1938), and *P. irradians* Lamarck (Gutsell 1930). However, Dalmon reported that the gonad of *Chlamys varia* L. resembles that of the edible oysters, with both male and female elements developing within the same follicle, the sexual phases being consecutive.

The sexuality of *Pinctada albina* is therefore not unique but has its counterpart in a variety of bivalve groups including the Ostreidae, Teredinidae, and Pectinidae, but the bivalves which the species resembles most closely are the oviparous (edible) oysters.

V. Discussion

(*a*) *The Breeding Season*

(i) *The Sampling Method.*—Stephenson (1934) contended that, for breeding season investigations, samples need not be large provided they are continuous and restricted to a certain area. On the average she examined 12 specimens per week, and considered that more would not have affected her conclusions except to give them greater precision. The author has used a similar number (20–25 specimens per fortnight) and agrees that such samples are large enough to show the seasonal trends,

TABLE 8

REPORTED BREEDING BEHAVIOUR OF PEARL OYSTERS

Species*	Restricted Breeding Season(s)			Continuous Breeding (with seasonal maxima)		
	Author	Breeding Season	Latitude	Author	Breeding Maxima	Latitude
Pinctada margaritifera	Nicholls 1931	Biannual: Nov. and May	10–17° S.			
	Ranson 1952	Summer (Oct.–Feb.)	13–25° S.	Seurat 1904*a*, 1904*b*	July–Oct. (slight variation)	13–25° S.
				Hervé 1931	Summer (Oct.–Feb.)	13–25° S.
	Crossland 1957	Summer (June–Oct.)	21° N.			
P. fucata (= *P. martensii* in Japan)	Craig, unpublished data, 1947	Midsummer (June–July)	34° N.	Herdman and Hornell 1906	Biannual: midsummer and midwinter (May–July; Nov.–Jan.)	7–10° N.
				Pearson, Malpas, and Kerkham 1929	As above	
P. maxima	Saville-Kent 1893	Summer	10° S.			
	Pace 1898	Biannual: Aug. and Feb.–Mar.	10° S.			
	Wada 1938, 1953	Summer (a small number spawn throughout the year)	10° S.	Talavera and Faustino 1931	May–Sept.	5–7° N.
				Hynd 1950	Oct.–Nov. (possibly also Feb.–Mar.)	10° S.
P. galtsoffi	Galtsoff 1933	Summer (July–Aug.)	27° N.			
P. maculata	Allen 1906	Spat settlement Feb.–Mar.	11° S.			
P. albina	Wada 1938, 1953	Oct. (possibly also Apr.–May)	10° S.			

*Nomenclature after Galtsoff (1933) and Hynd (1955).

provided the values are smoothed in some way; however, he would hesitate to use samples of this size to determine the sequence of events within a restricted period, for example, intermittence of spawning.

(ii) *Other Observations on the Breeding Season of* P. albina.—The only observations previously made on this species were of a restricted nature and concerned the specimens found attached to the silverlip pearl oyster, *P. maxima*, in north Australian waters (Wada 1938, 1953). The gonad was well developed in July and August, and in October spawning was observed. Unfortunately such isolated observations are of little value with this species, and may or may not indicate that there was a spawning maximum at that time. Wada (1938) suspected there might be another spawning season in April or May, but since his observations ceased in November, he seems to have been influenced in this opinion by the work of Herdman and Hornell (1906) and Nicholls (1931), who reported biannual breeding in other pearl oyster species.

(iii) *The Breeding Season of Other Pearl Oysters.*—As Table 8 shows, there is considerable difference of opinion as to whether the various species of pearl oysters have a continuous or a restricted breeding season. The evidence does suggest, however, that in higher latitudes the breeding season is more restricted, and occurs during the warmer months (for example, *P. martensi*, Japan, 34° N.; *P. galtsoffi* Bartsch, Hawaii, 27° N.; and *P. margaritifera* L., Red Sea, 21° N.), while in lower latitudes there is a less restricted breeding season, and major spawnings occur outside the warmer months (for example, *P. margaritifera*, Low Isles and Torres Strait, 17° S. and 10° S.; and *P. fucata* Ceylon, 7–10° N.).

(iv) *Breeding in the Tropics.*—Semper (1883) noted that in the tropical Philippines, freshly deposited eggs and young (of marine invertebrates) could always be seen, and he concluded that there was "a total absence of periodicity" in breeding. Orton (1920), largely influenced by Semper's observations, stated: "In those parts of the sea where temperature conditions are constant or nearly so, and where biological conditions do not vary much, animals will breed continuously. This is apparently so in the tropics."

The first exhaustive test of this theory was made by Stephenson on the Great Barrier Reef where she investigated the breeding habits of 10 species representing widely diverse invertebrate groups. She concluded (Stephenson 1934) that in the tropics, spawning takes place throughout the year, but that the majority of species spawn either exclusively or most actively during the warmer months. So far as tropical pearl oysters are concerned, and *P. albina* in particular, there is certainly a tendency toward continuous breeding, but there is less correlation between breeding and high temperatures than there is in allied species and populations outside the tropics. This may mean that there is a critical temperature for breeding in pearl oysters, and that this temperature is reached in higher latitudes only during the summer, but in lower latitudes is exceeded all the year round.

(*b*) *Sexuality*

Orton (1927*b*), largely influenced by the work of Goldschmidt (1923) concerning mechanisms of sex determination, put forward a theory, for bivalve groups experiencing sex change, that metabolic rather than genetic factors determine sex. He suggested

that sex change in *O. edulis* is due to a metabolic rhythm in two phases: (i) a protein metabolism accompanied by egg development; (ii) a carbohydrate metabolism associated with the development of sperm. The accumulation of non-usable products of one kind of metabolism above a certain concentration was thought to be the stimulus for the change-over. However, there has not been any substantial evidence in favour of Orton's theory, and Couteaux-Bargeton (1947) has shown that in *C. angulata* at least, there is no essential difference between the types of metabolism of male and female. Nevertheless, many workers have shown that better environmental conditions favour the female phase (Sparck 1925; Amemiya 1928, 1935; Awati and Rai 1931; Needler 1932; Coe 1936*b*). Roughley (1933) tested this theory on the Sydney rock oyster *C. commercialis*, by comparing the sex ratios from "good" and "poor" grounds. He found no essential difference, but since he did not specifically choose samples of the same approximate age, such comparisons are of little value.

The evidence suggests that the sex-determining mechanism must be very labile if the animal is able to react to its environment to achieve the sexual phase more suited to its physiological condition. However, there are certain features of sexuality in this group which do appear to be genetically determined: (i) the inherent tendency toward protandry; (ii) the tendency toward rhythmical change of sexual phase. But is there any need to invoke a hereditary explanation? It would seem that there are too many individual variations from these tendencies, and that it is more likely that the bivalve inherits the lability, or freedom, firstly, to develop either as one sex or the other, and secondly, to respond differentially to good and bad environmental conditions. Coe (1943) suggests that there are hereditary modifying factors for the activation or suppression of either the male or female determining components at certain stages of development, and that these components are responsive to the environmental conditions.

The present author questions the existence of hereditary modifying factors, and puts forward the following theory to explain the observed sexual phenomena.

It is likely that the development of the female gonad, involving the storage of yolk and its consequent loss at spawning, utilizes a greater proportion of the food reserves of a bivalve than does development of the male gonad. Should this be so, then individuals with low food reserves would reproduce less effectively as females than as males. It is suggested that the germ cell rudiments respond to the food reserve level by differentiating toward maleness at lower levels, and toward femaleness at higher levels.

Such a theory would explain why sickness, parasitic infestation, injury, pollution, malnutrition, and other environmental factors affecting the physiology of a bivalve are able to influence its sex; further, should the food level be low during early growth, as seems likely, then it would also explain why primary gonad development is usually male, the female phase following when growth slows down somewhat. Similarly, protogynic sex change could be explained on the basis of a low food reserve level after female development.

It is interesting to conjecture, in view of this theory, what effect the presence of unspawned gonad products would have on the sex of the succeeding phase.

VI. Acknowledgments

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EXPLANATION OF PLATE 1

Fig. 1.—Bisexual gonad, showing how both male and female germ cells develop within the same gonad follicle. ×75.

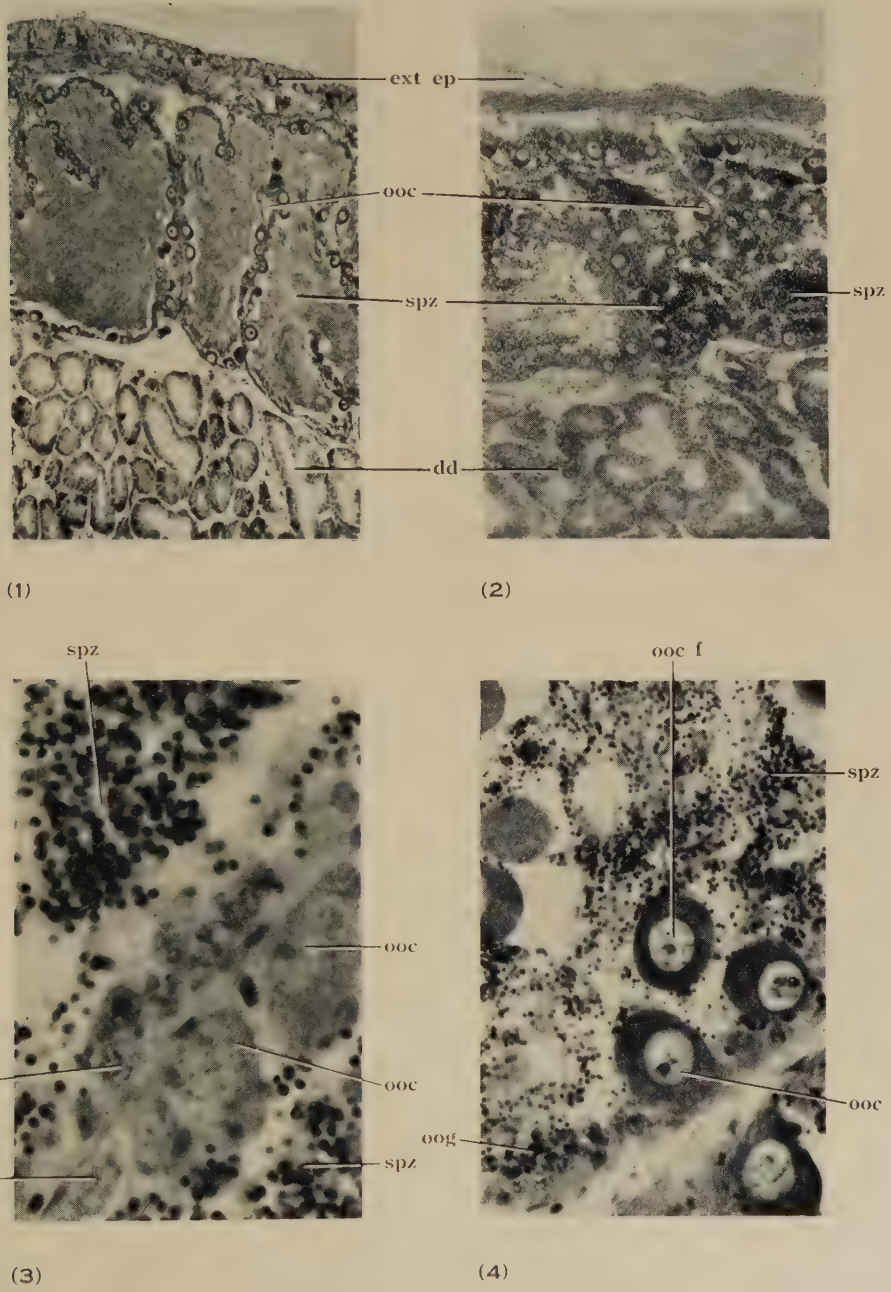
Fig. 2.—As above. ×100.

Fig. 3.—Bisexual gonad: early female development, early male regression. ×1000.

Fig. 4.—Bisexual gonad: advanced female development, early male regression. ×400.

dd, Digestive diverticula; *ext ep*, external epithelium; *oog*, oogonia; *ooc*, oocyte; *oocf*, free oocyte; *s*, stem cell; *spz*, spermatozoa.

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. III



A GENERAL ACCOUNT OF THE INTERTIDAL ECOLOGY OF SOUTH AUSTRALIAN COASTS

By H. B. S. Womersley* and S. J. Edmonds†

[*Manuscript received July* 22, 1957]

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Summary

An account is given of the environmental features, the intertidal ecology, and the biogeographical relationships of the coast of the State of South Australia.

The central and western coasts of South Australia are similar ecologically in comparable areas. In the supralittoral *Melaraphe unifasciata* (Gray) is dominant (except where conditions are very calm) and at high levels on very exposed coasts

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Calothrix fasciculata C. Agardh is found. The littoral zone where the coast is most exposed consists of barnacles—*Chamaesipho* in the upper littoral, *Catophragmus* in the mid littoral, and *Balanus* in the lower littoral—but where the coast is more sheltered it consists of molluscs in the upper and mid littoral and algae (*Corallina*, *Gelidium*, or *Hormosira*) in the lower littoral. In the upper sublittoral fucoid algae or in calm regions marine angiosperms are dominant. The south-east coast, however, differs in some respects from the central and west coasts. The number of barnacles found in the littoral zone is much reduced and the giant brown algae, *Durvillea potatorum* Areschoug and *Macrocystis angustifolia* Bory, are dominant in the upper sublittoral. This is associated with slightly lower sea temperatures.

Sheltered coasts are more prominent in South Australia than in the eastern States of Australia. These include the shores of Spencer and St. Vincent Gulfs, the northern shores of Kangaroo I., and a number of scattered bays.

The similarities between the coasts of South Australia and Victoria (Bennett and Pope 1953) are greater than the differences. Consequently the proposal of Bennett and Pope to recognize the Victorian and Tasmanian coasts as the Maugean Biogeographical Province and the South Australian and the south-west Western Australian coasts as the Flindersian Province appears to be unjustified. It is suggested that the Maugean is best regarded as a subprovince with the Flindersian. The latter includes most of the coast of southern Australia.

Considerable differences are noticeable between the organisms which inhabit the rocky coast of South Australia and the south coast of Western Australia. The available evidence indicates that a transition from the Flindersian to the tropical Dampierian Province occurs along the south and west coasts of Western Australia. The terms "Indo-Australian Province" and "Baudinian Province" have been proposed by previous authors to describe this transitional region.

The Flindersian Province appears to be intermediate between cold-temperate and warm-temperate regions, becoming distinctly cool-temperate in Tasmania. It is relatively distinct from the warm-temperate Peronian Province of the coast of New South Wales.

I. Introduction

Ecological surveys of the coast of South Australia over the past 10 years have reached a stage where a general account of the marine intertidal ecology can be given. The first zoological survey of the coast near Adelaide was that of Johnston and Mawson (1946). Early work by the present authors (Womersley 1947, 1948; Edmonds 1948) was concentrated on Kangaroo Island, because this showed almost the full range of environmental conditions found along the South Australian coast. Since then the rest of the coastline (some parts of which are rather inaccessible) has been studied in somewhat less detail. Two field trips (both during January and February) have been made along Eyre Peninsula as far west as Fowler's Bay, one being extended to Eucla. The coast in the south-east of the State, extending into Victoria, is better known from visits at different times of the year. Most field work in South Australia must be done during the summer months, since the sea-level in winter is significantly higher than in summer, and in winter the lowest tides occur during the night.

Studies in recent years by Dakin, Bennett, and Pope (1948) in New South Wales, Bennett and Pope (1953) in Victoria, and Endean, Kenny, and Stephenson (1956) in Queensland have given the general picture of the intertidal zonation in these States. Certain localities in Tasmania have been described by Guiler (1951, 1952*a*, 1952*b*, 1954) and Cribb (1954). The Western Australian coast is known only from

unpublished M.Sc. theses of G. G. Smith (algal emphasis) and Mrs. L. Marsh (animal emphasis), and observations and collections made by Miss E. Wollaston, of the Botany Department, University of Adelaide, on a field trip from Rottnest Island to Esperance in February 1957.

This paper aims at giving a general account of the South Australian coastline, linking with Bennett and Pope's account of Victoria and with what is known of the Western Australian coast. The biogeographical provinces of southern Australia are also discussed.

The accounts of Dakin, Bennett, and Pope (1948) in New South Wales, Bennett and Pope (1953) in Victoria and Endean, Kenny, and Stephenson (1956) in Queensland, deal intentionally only with rocky coasts. Such coasts probably comprise most of the eastern Australian shores (apart from sand beaches). In South Australia the gulf region, with sheltered waters, and sandy or muddy intertidal areas and rocky outcrops in the northern parts, is of considerable importance. Together with calm bays and inlets (such as American River inlet on Kangaroo I. (Womersley 1956)) these areas form a distinctive part of the coastal ecology, and considerable attention has been given them. Long stretches of sandy beach and smaller sandy bays are common in South Australia.

The rough conditions on exposed coasts and tidal irregularities prevent accurate correlation of zones of organisms with tidal levels. Studies on Kangaroo I. gave an adequate conception of where the zones lay in relation to tidal levels, and the zones and ecology in other areas were studied mainly by reference to indicator organisms disclosed in earlier work. Transects were used in early studies where necessary. Basic to broad ecological studies is the realization that the intertidal organisms are reacting to their whole environment, of which tidal exposure is only one factor. Indicator organisms, once their position and prominence are established, form the best basis on which accounts of zonation on brief coastal visits can be given.

The flora plays a considerably more prominent part in this account than in those of the eastern Australian workers. The reasons for this are, firstly, that the algae and marine angiosperms are probably more important in southern Australia than on eastern Australian coasts; and, secondly, that one of the present authors is an algologist. The only other account of Australian algal ecology is that of Cribb (1954), who describes Port Arthur, Tas. The general picture of Australian intertidal ecology that has emerged in recent years is more adequate on the faunistic side than on the floristic.

Many more animals were collected during field trips than those mentioned in this paper. Attention has been given chiefly to those which were important ecologically. Thanks to the help of a number of specialists most animals except those belonging to the Porifera and the Bryozoa have been identified. Efforts have been made to obtain specific nomenclature uniform with that of other Australian workers in shore ecology. It is well known that some animals (particularly the molluscs) show considerable variation within a species. This has made rather difficult in a few cases the task of naming closely related or possibly identical species collected from localities 500–1500 miles apart.

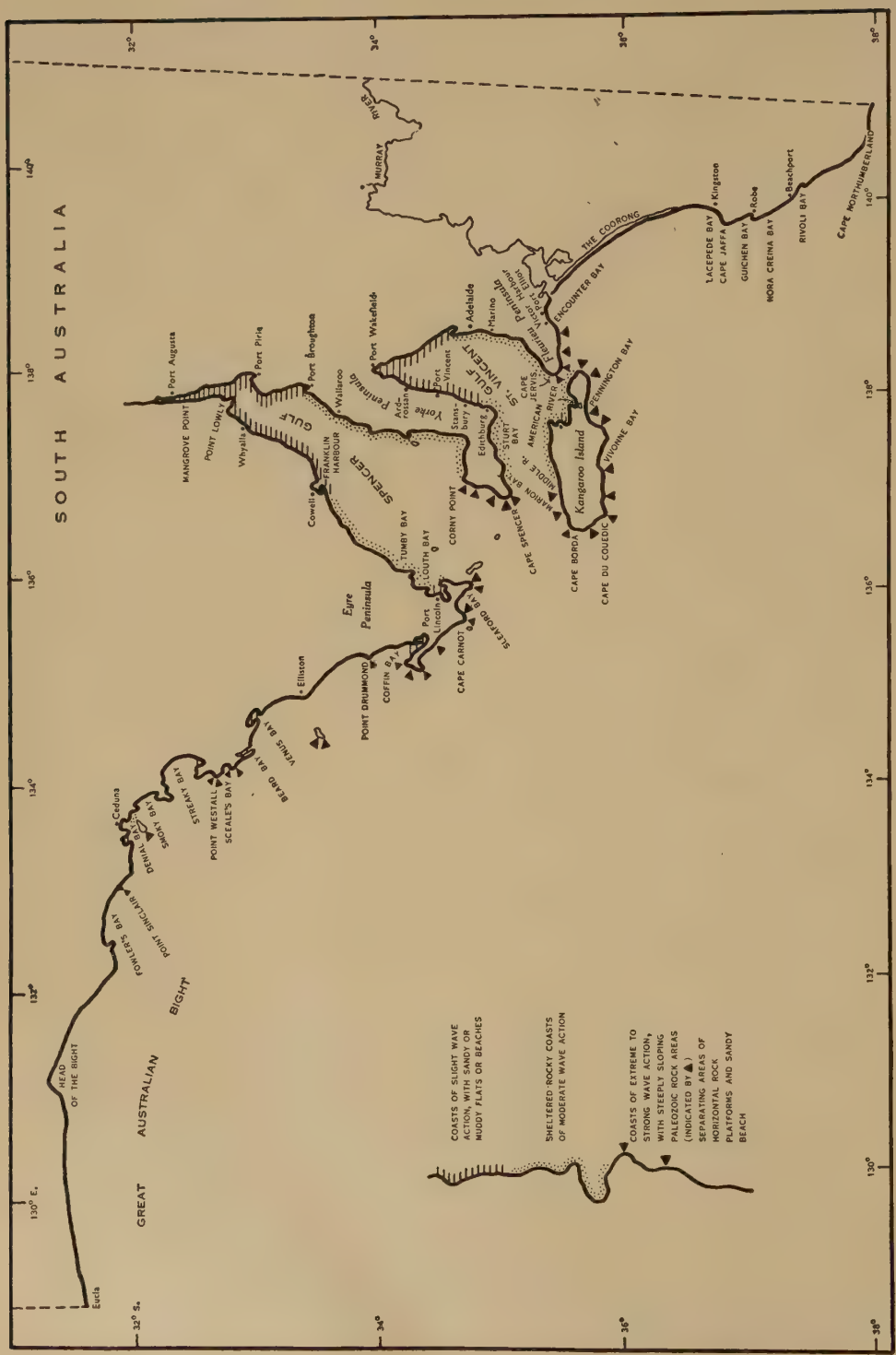

Fig. 1.—Map of South Australia, showing the broad classification of the coastline based on the intertidal ecology, and also most of the localities which were studied during the survey.

II. Environmental Features

(a) *Coastal Geology and Topography*

Much of the South Australian coastline is of Recent or Pleistocene age and consists of beach sands and dunes which in many areas have become consolidated to form calcareous sand-rock cliffs and reefs. This coastline is usually "supported" by capes or headlands of more resistant Palaeozoic rocks such as quartzites and schists or of igneous rocks such as granites.

The coastal features are shown in the accompanying map (Fig. 1, after the Geological Map of South Australia of 1953).

The south-eastern region, from Encounter Bay to the Victorian border, consists of a continuous sandy beach from Port Elliot to Robe, then alternating areas of Pleistocene sand-rock cliffs and reefs and loose sandy beaches. In the extreme south-east the cliffs and reefs are of Recent to Upper Oligocene age.

Fleurieu Peninsula, from Encounter Bay to Cape Jervis, comprises steep cliffs of Palaeozoic rock. Lower cliffs or stony beaches occur in calmer areas of Gulf St. Vincent from Cape Jervis to Marino.

On Kangaroo I. the south and west coasts consist of capes and headlands of Palaeozoic rocks, between which are extensive areas of sand-rock cliffs and sand beaches. The north coast is formed of Palaeozoic rocks, with high cliffs in the west and low land in the east. Sandy and muddy tidal flats are found in American River inlet and other parts of Nepean Bay.

The gulf region, including St. Vincent and Spencer Gulfs, is of Palaeozoic rock in the more exposed southern parts, which are similar to the south coast of Kangaroo I. The upper half or more of the gulfs is of Recent age and sandy-muddy beaches and tidal flats have developed under calmer conditions.

The south-west of Yorke Peninsula, and the south and whole west coast of Eyre Peninsula, extending almost to the head of the Great Australian Bight, are formed of Recent or Pleistocene calcareous sand-rock cliffs or sand beaches, supported by granitic points. From the head of the Bight westwards to the Western Australian border the coast is of Pliocene age; for 50 or more miles east of the head of the Bight it is sandy beach, backed by high sand dunes. West of the head of the Bight the Nullabor Plain reaches the sea, with calcareous cliffs up to 400 ft high dropping sheer to wave-cut platforms.

The coastal topography thus falls into four classes:

(1) Steeply sloping Palaeozoic rocks, often granite, schists, or quartzites, dropping fairly steeply into deep water on rough coasts, less steeply under calmer conditions.

(2) Calcareous sand-rock cliffs of Recent or Pleistocene age, which form wave-cut platforms at low tide level.

(3) Sandy beaches between calcareous platforms or areas of older rock.

(4) Sandy or muddy tidal flats, developed in bays or inlets or in the upper part of both Gulfs.

(*b*) *Degree of Wave Action*

Coastal waters in South Australia vary from very rough with constant breakers on exposed coasts to a "dead calm" in fully protected areas.

Coastline fully exposed to the south or west is subject to the prevailing winds from the same direction, and a heavy surge or lines of breakers up to 6 ft high or more are typical. Only on fairly calm days with an offshore wind are conditions greatly moderated, and such days occur only a few times during summer. The accompanying map shows that most of the South Australian coastline falls into this category, except the gulf region, the north coast of Kangaroo I., and small bays along otherwise exposed coast.

Within the gulf region, and along the north coast of Kangaroo I., a grading in degree of wave action occurs from exposed coast to strongly sheltered or land-locked areas. Thus conditions become calmer proceeding north in both gulfs, while the west coast in each gulf is calmer than the east, since winds are predominantly from the west. The calmest part of the north coast of Kangaroo I. is the almost land-locked area of American River inlet. Here wave action is almost negligible on the tidal flats except when strong winds blow across the lagoons. Other bays similar to American River inlet are Proper Bay (Port Lincoln), Franklin Harbour, parts of Coffin Bay, Venus Bay, Beard's Bay, and parts of Streaky Bay and Denial Bay.

The grading of wave action along coasts with otherwise similar environmental features (e.g. north coast of Kangaroo I.) provides an interesting series of ecological changes showing clearly the important effect of degree of roughness. Unfortunately objective measurement of wave action is seemingly impossible. As well as average conditions, extreme conditions over short periods are of great importance. The personal factor is always considerable in any estimate of wave conditions, and particularly on brief field surveys much latitude must be allowed for variation from conditions observed. It is frequently better to use indicator organisms to compare the degree of wave action in different areas. The height of zones and of rock pools can also be useful. The presence of rock pools with marine species some 100 ft above sea-level at Cape Bridgewater, near Portland in Victoria, indicates the extreme roughness of this locality. Here the cliffs descend vertically into very deep water. No area in South Australia has been seen which is comparable to Cape Bridgewater in these respects.

(*c*) *Tides*

Tides along the South Australian coast are of relatively small amplitude and may show considerable variation from place to place.

On exposed coasts the spring range is about $2\frac{1}{2}$–4 ft, increasing to 4–5 ft on the north coast of Kangaroo I., to about 6 ft in the lower gulfs, 9–11 ft at the head of Gulf St. Vincent, and 12 ft at Port Augusta at the head of Spencer Gulf. The height of the tide may be greatly modified by winds. On exposed coasts, a strong offshore wind keeps the sea-level down and invariably gives the best collecting conditions. Within the gulfs the contour of the coast, and local winds, are important. At Port Augusta south-west winds send up the highest tides, while at Port Adelaide north-west winds have the greatest effect.

The tides at American River inlet during 1950 have been analysed by Womersley (1956). Many features apply generally to other parts of South Australia where conditions are not rough. The tides are considerably more irregular than in many parts of the world. At spring periods the tides are semidiurnal, but the two daily tides may vary from almost equal to markedly unequal amplitude. The highest tides usually occur between 0 and 3 days after new or full moon but may occur at other times. The lowest tides of the spring period rarely occur at the same time as the highest tides, but are most irregular. In fact, the lowest tides more often occur at the "dodge" periods.

At neap periods, the "dodge" effect occurs in many parts of South Australia, especially in the gulf region (Chapman 1924). In most cases only one tide per 24 hr occurs over 2–4 days at the neap period, but two tides of lesser amplitude may occur. Particularly in parts of the gulfs a more typical dodging tide may occur, during which the water level is almost stationary (subject to wind) for up to 24 hr. When the single tide occurs, the low level is usually lower than tides before and after, while the high may be nearly as high as some spring tides. The neap period varies from a day before the first and third quarters of the moon to 4 or 5 days after.

Mean sea-level, and other tidal means, are highest during the winter and lowest during the summer months, the difference being as much as 6–8 in. January–February is the period of the lowest sea-level and thus the lowest tides.

In general, the lower of the two daily low tides occurs during the middle of the day in summer (October–April) and in the middle of the night from June to September. The higher of the two daily low tides occurs in the early hours of the morning during summer, and in the afternoon during the winter. The lower of the high tides is the opposite of this.

Thus both the lower sea-level in summer and the time of the lowest tide make the summer months, especially January–February, most suitable for intertidal studies, and often prohibit work during the winter. The calmer conditions and more frequent offshore winds during summer also help field work.

(*d*) *Currents*

Most publications (e.g. "Australia Pilot", Vol. 1 (1937)) refer to a slow drift from west to east. Halligan (1921) describes how the cold Southern Ocean current bifurcates south-west of Cape Leeuwin, one part flowing northwards along the west coast of Western Australia and the other flowing eastwards along the south coast as far as Bass Strait. A warm current from the Indian Ocean also passes around Cape Leeuwin and flows eastwards across the Great Australian Bight as a surface current, above the cold Southern Ocean current. These currents mix in the vincinity of Tasmania, accounting for the cooler water in Bass Strait. Little is known, however, of currents near the coast in the region of the Great Australian Bight. The best recent information is the series of charts published by the Royal Netherlands Meteorological Institute (1949). These give little data for the continental shelf waters of the Great Australian Bight, and indicate the very variable nature of the currents off the shelf. There is clearly no sustained current along the shore of southern Australia, although the general tendency is probably for a slow drift from west to east, subject to variable

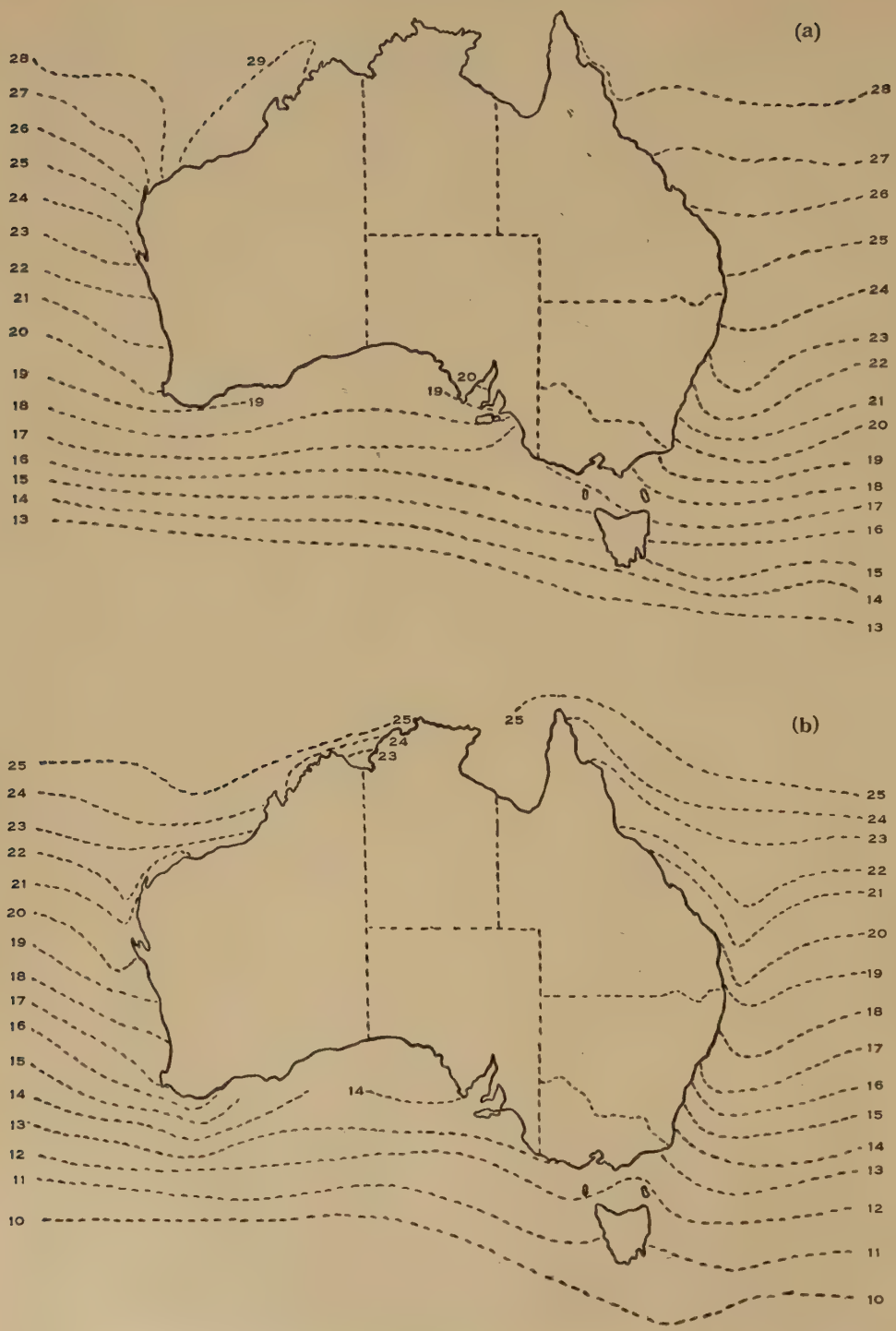

Fig. 2.—Mean sea temperatures around Australia during (*a*) February, and (*b*) August.

local counter-currents. From April to November there is a slight easterly current around south-west Western Australia, but not for the rest of the year. The 18th Annual Report of the Council for Scientific and Industrial Research (1944), which refers to results of drift-bottle experiments in Western Australian waters, indicates a flow southward around Cape Leeuwin and eastwards along the south coast in winter, and a reversal of this flow in summer.

(*e*) *Winds*

Winds blow mainly from directions between west and south, but are greatly influenced on the coast by local sea breezes. Northerly winds in summer are of the greatest importance. On a hot day (up to 100°F shade temperature) with an offshore wind (usually northerly) the sea-level is depressed, and should the wind be strong enough or coincide with a low tide, organisms at a low littoral level may be exposed for several hours and suffer considerable harm. Extensive areas of *Hormosira* and fucoids on reefs have been seen blackened and often killed under these conditions. While such conditions usually occur on only a few days in summer, they may be of importance in limiting the intertidal growth of many species.

(*f*) *Sea Temperatures*

The charts of the Royal Netherlands Meteorological Institute (1949), reproduced in Figures 2(*a*) and 2(*b*), give the best picture of sea temperatures along southern Australia. The sea temperatures from south-west Western Australia to south-east South Australia differ little at any one time of the year.

Few figures are available for the region of the Great Australian Bight, but isolated temperatures taken by the present authors during summer as far west as the head of the Bight were much the same as those known to occur on the south coast of Kangaroo I. The isotherms probably follow the contour of the coast in the central parts of southern Australia.

Temperatures just off exposed coasts are 18–20°C in summer and 14–16°C in winter. In the south-east of South Australia temperatures are lower in summer by 2–3°C, but only 1° or so lower in winter (Figs. 2(*a*) and 2(*b*)). This region of lower temperature has been emphasized by Bennett and Pope (1953) in describing Victorian shore ecology, and its significance is discussed later. Bennett and Pope separated the cooler Victorian and Tasmanian coasts from those of New South Wales and South Australia. They did not point out, however, that the uniform temperatures along the rest of southern Australia are matched by those on a relatively small region of the eastern Australian coast, just below and for 100–150 miles north of the Victorian–New South Wales border. Most of the New South Wales coast is subject to distinctly higher temperatures than that of southern Australia.

Sea temperatures within the gulf region are higher in summer and lower in winter than on rougher coasts, and show greater variation. Summer temperatures of up to 25°C or even to 30°C on shallow flats occur in the northern part of the gulfs or in shallow bays and inlets.

On exposed coasts the intertidal organisms when submerged are subject to much the same temperatures as that of offshore water. Air temperatures become important

for intertidal organisms during low tide. Rock pools, and shallow water on calmer shores, are subject to a greater range of temperature.

(g) *Air Temperatures and Relative Humidities*

The information shown in Table 1 was obtained from a publication of the Commonwealth of Australia (Australia, Bureau of Meteorology 1956). Data for January and July have been given as representing conditions in midsummer and midwinter respectively.

The information included in the table shows: (i) that the mean maximum daily temperature during summer and the seasonal variation of daily temperatures are much greater at localities along the coasts of the gulfs than along the open coast; (ii) that the mean minimum daily temperatures during winter along the open coast do not differ

TABLE 1

AIR TEMPERATURES AND RELATIVE HUMIDITIES AT FOUR COASTAL LOCALITIES

Locality	Long. (E.)	Lat. (S.)	Average Daily Maximum Temperature (°F)		Average Daily Minimum Temperature (°F)		Average Relative Humidity (%) at 3 p.m.	
			Jan.	July	Jan.	July	Jan.	July
Fowler's Bay	132° 49′	31° 59′	76·2	62·7	63·0	44·5	65	59
Port Augusta	137° 45′	32° 29′	89·5	62·8	65·3	43·9	33	52
Adelaide	138° 35′	34° 56′	84·8	59·9	61·0	45·4	31	61
Cape Northumberland	140° 40′	38° 5′	69·2	56·2	55·6	44·6	66	74

very much from those along the gulf coasts; (iii) that the seasonal variation of relative humidity is much greater along the gulf coasts than along the open coast. Temperatures are lower and humidity higher at Cape Northumberland in the south-east of South Australia than at the other localities. On exposed coasts the constant spray blown over the intertidal region must keep conditions moist, but again the extreme conditions of hot dry winds combined with low tides in summer are of importance. No measurements of humidity close to organisms in the intertidal region are available. On calm coasts low humidity would be expected during summer months.

(h) *Chlorinity, Phosphate, and Nitrate*

The available information about the chlorinity of sea-water in South Australia has been summarized by Thomas and Edmonds (1956). The chlorinity of surface samples varies from 19·00 to 20·25‰ off the open coasts to as high as 26‰ at Port Augusta. The little evidence available (Howard 1940; Thomas and Edmonds 1956) indicates that the amount of phosphate and nitrate in the sea water is low.

(i) *Dissolved Oxygen*

A number of estimations have shown that the oxygen saturation of sea-water on rough coasts varies from 95 to 110 per cent. The degree of saturation of still

water is more variable. Values of 100–200 per cent. (commonly about 130) saturation were recorded during the day for water covering extensive algal growth, and corresponding values of 50–60 per cent. saturation during the night.

III. Terminology and Nomenclature

The zonation terminology used in this paper has been described and discussed previously (Womersley and Edmonds 1952) and is only outlined briefly here. It closely resembles that used by many other marine ecologists (e.g. Gislen 1930; Feldmann 1951).

Within the intertidal and subtidal regions three main zones can be distinguished (Table 2). These are primarily due to tidal fluctuations, modified to a varying extent by other environmental factors such as the degree of wave action and the aspect of the shore. While the limits of these zones correspond (more or less) to tidal limits and means, in many cases it is more convenient to use indicator organisms to distinguish the zones. Correlation between tidal factors and zones of organisms has been studied in South Australia only at American River inlet on Kangaroo I. (Womersley 1956). Unfortunately adequate correlation is very difficult on exposed coasts subject to a small tidal rise.

Indicator organisms are of great importance in delimitating zones in that they (like all organisms) are reacting to their total environment.

The following basic zones are recognized:

(i) *The Supralittoral Zone.*—This extends from the top of the littoral to the upper limit of marine organisms. Here the littorinid *Melaraphe* is dominant on most South Australian coasts and the lichens *Lichina* and *Verrucaria* are often common.

(ii) *The Littoral Zone.*—This is the main intertidal region, which extends from the sublittoral to about high water level or to the upper limit of prevalent wave-wash. This upper limit is difficult to fix satisfactorily on physical factors, and the present authors (like most workers) have used the upper limit of certain small barnacles or other indicator organisms to determine it. The lower limit of *Melaraphe* often corresponds roughly with the upper barnacle limit.

Within the littoral, three subzones can be conveniently distinguished on South Australian coasts:

(1) *The upper littoral,* dominated by barnacles or various molluscs.

(2) *The mid littoral,* dominated by barnacles on rough coasts and by molluscs, serpulids, or blue-green algae under less extreme wave action.

(3) *The lower littoral,* dominated by algae.

(iii) *The Sublittoral Zone.*—This extends from about mean low water neaps downwards (to the limit of algal vegetation). This zone is distinguished in South Australia by brown algae such as *Cystophora*, *Sargassum*, and *Ecklonia*. The uppermost margin of the sublittoral may be exposed for short periods at extreme low tides or during the suck-back of waves.

Upper sublittoral is used for the region where larger brown algae are dominant; it usually extends down for some distance below the lowest low tides.

TABLE 2

SUMMARY OF INTERTIDAL ZONATION ON SOUTH AUSTRALIAN COASTS

Zone	Western and Central Coasts					South-Eastern Coast
	Extreme to Strong Wave Action			Moderate Wave Action	Slight Wave Action	Extreme to Strong Wave Action
	Steeply Sloping Palaeozoic Rock	Horizontal Rock Platforms	Sand Beaches	Sheltered Coasts	Sandy or Muddy Flats	Horizontal Rock Platforms
Supralittoral	*Calothrix* ..... *Melaraphe*	*Melaraphe* *Lichina* *Verrucaria*	*Talorchestia*	*Melaraphe* *Lichina*	Relatively bare when rocky Samphires	*Melaraphe* *Lichina* *Verrucaria*
Upper littoral	(*Chthamalus*) *Chamaesipho*	*Chthamalus* *Chamaesipho*	Isopods	*Chthamalus* *Chamaesipho*	Samphires, mangroves, or *Bembicium*	
Mid littoral	*Catophragmus* (Molluscs, *Galeolaria*, blue-green algae)	(*Catophragmus*) Molluscs, *Galeolaria*, blue-green algae *Brachyodontes rostratus*		Molluscs, *Galeolaria*, blue-green algae	*Bembicium*, *Modiolus inconstans*, mangroves, Enteromorpha	Molluscs, *Galeolaria*, blue-green algae
Lower littoral	*Balanus* – coralline mat	*Hormosira* Other algae	Bivalves	*Corallina* – *Gelidium*, *Hormosira*	*Hormosira* *Brachyodontes erosus*, *Katelysia*, *Pinna*	*Hormosira*
Sublittoral fringe	*Cystophora intermedia*	*Cystophora intermedia*		*Cystophora* sp. ↓	*Hypnea*, *Spyridia*, and other algae	*Durvillea* ↓
Upper sublittoral	Fucoid algae etc.	Fucoid algae, *Ecklonia*, red algae	Bivalves	Other algae	*Zostera* ↓ *Posidonia* ↓	*Macrocystis* ↓

Sublittoral fringe conveniently describes a zone often found at the upper margin of the sublittoral, extending down to extreme low water or to the lower limit of the suck-back of waves. This term is used in the original sense of Stephenson (1939), not in the broader sense (equivalent to upper sublittoral) of other workers.

This terminology has been used in papers on South Australian marine ecology (Womersley 1947, 1948, 1956; Edmonds 1948); and in recent papers on the Victorian coast by Bennett and Pope (1953) (although referred to Stephenson's (1949) scheme) and on Tasmania by Cribb (1954). The account of Womersley and Edmonds (1952) which discussed the terms and nomenclature proposed by Stephenson and Stephenson (1949) has been criticized by Chapman and Trevarthen (1953) and Guiler (1953). However, Chapman (1956, p. 335) in a more recent paper uses zonation terms closely similar to those supported by the present authors.

Within the zones, associations or communities can be recognized. Distinct groupings of one or more species may be termed associations, while less distinct groupings are referred to as communities.

The coast of Kangaroo I. was classed by Womersley (1947) into two formations, following Cotton (1912):

(1) Rocky coast formation, subdivided into exposed and sheltered subformations.

(2) Sand and sandy-mud flat formation.

Similar divisions of the coast are used in this paper, since they describe the main coastal types found in South Australia. Whether they be termed "formations" or not is of no great consequence; they can equally well be referred to as "types" of coast or by other noncommittal terms. This concept of "formation", based on both habitat and life form (lithophilous, holdfast-possessing algae on rocky coast and stoloniferous sea-grasses or algae on sandy or muddy flats) is probably closest to the use of "formation" as a major unit in land ecology.

IV. Intertidal Ecology

The following account deals first with the western and central parts of the South Australian coastline, and later with the south-east coast of the State (from Robe eastwards). The latter is similar to the Victorian coast and shows certain differences from areas of South Australia further west. These two coastal regions are separated by some 120 miles of sandy beach. The importance of the differences between the south-east coast and the central and west coasts of South Australia is discussed later in this paper.

A. the western and central coasts

These areas, comprising all the coastline west of Port Elliott, fall into two major types, with convenient subdivisions, dependent on degree of wave action and nature of the substratum. These two factors are, of course, partly interdependent.

The following types of coast are recognized (see Table 2):

(*a*) Coasts of moderate to extreme wave action; rocky with sandy beaches interspersed.

(i) Coasts of strong to extreme wave action.

(1) Steeply sloping intertidal regions of Palaeozoic rock.

(2) Horizontal intertidal rock platforms.

(3) Sandy beaches (on the open coast).

(ii) Sheltered coasts of moderate wave action.

(*b*) Coasts of slight wave action, with sandy or muddy flats or beaches.

Since the nature of the substratum and degree of wave action are the two most important factors controlling the occurrence of marine organisms, these divisions are both convenient and natural ones, characterized by distinctive communities or species. There is, of course, grading between these coastal types, particularly within the gulf region. Calm areas are often found on rough coasts where there is local shelter. The sheltered side of large boulders will likewise often show zonation more characteristic of sheltered coasts.

The map (Fig. 1) shows the approximate extent of these coastal types. Small calmer areas on rougher coasts cannot be shown on a map of this scale.

Rocky coast (interspersed with sandy beaches) with strong to extreme wave action comprises all the coastline exposed to prevailing winds from over deep water—the Great Australian Bight, the west coast and southern tip of Eyre Peninsula, the southern ends of Yorke and Fleurieu Peninsulas, the south and west coasts of Kangaroo I., and the south-east coast of the State. Rocky coasts of moderate wave action include the southern parts of Spencer and St. Vincent Gulfs and the north coast of Kangaroo I. Coasts of slight wave action, with sandy or sandy-mud flats, comprise the northern parts of the gulfs (excluding rocky outcrops), and several almost land-locked bays scattered along rougher coasts, such as parts of Denial Bay and Streaky Bay, Beard's Bay, parts of Coffin Bay, Proper Bay in Port Lincoln, and American River inlet on Kangaroo I.

(*a*) *Coasts of Moderate to Extreme Wave Action; Rocky with Sandy Beaches Interspersed*

(i) *Extreme to Strong Wave Action.*—These coasts are continually subject to successive lines of breakers and heavy spray. The only relatively calm periods occur occasionally during summer when strong offshore winds blow; then the intertidal region is subject only to low waves.

(1) *Steeply Sloping Intertidal Regions of Palaeozoic Rock.*—Palaeozoic rocks—granite, schists, gneisses, etc.—form the exposed headlands and capes along the South Australian rough coastline, as shown in the accompanying map. Rock in the intertidal region varies from smooth granite, sloping steeply into deep water (e.g. Point Sinclair, Plate 1, Fig. 1), to broken masses of rock presenting a variety of microhabitats. The smooth rock faces are more common and show clearer zonation than the broken areas. Where waves surge up smooth rock for a considerable height, the intertidal zonation may be spread over a vertical height of up to 30 ft (Plate 1, Fig. 1), with well-defined and sharply limited zones.

Good examples of such areas are Point Sinclair and Cape Carnot on the west coast of Eyre Peninsula, and Cape Du Couedic and the south side of Point Ellen, Vivonne Bay, on Kangaroo I.

Supralittoral zone

On smooth rock faces with extreme wave action and considerable spray, two subzones occur; under less extreme conditions the upper subzone may not be present.

Upper supralittoral.—The blue-green alga *Calothrix fasciculata* C. Agardh forms an extensive black covering on the rock, from a few feet above the highest barnacles upwards for 6 or 10 ft vertically. This zone is particularly well developed at Point Sinclair (Plate 1; Plate 2, Fig. 1), less so on the south side of Point Ellen, Vivonne Bay, but is often absent if conditions are less extreme or the substratum is more dissected.

The upper edge of the *Calothrix* association fades out, but the lower edge is irregular and sharply defined. Clear areas of rock with similar sharply defined edges occur within the association (Plate 1, Fig. 2). In each of these a small crevice or slight depression retaining moisture is found, inhabited by a cluster of *Melaraphe unifasciata* (Gray). The sharp and irregular edge of these "*Melaraphe* patches" and the similar lower edge of the association are probably due to feeding of the *Melaraphe* (during or after high tide, or at night). It is possible that the *Melaraphe* is unable to obtain a foothold on the slippery *Calothrix* mat.

Lower supralittoral.—This zone, lying between the *Calothrix* association and the barnacles of the upper littoral, is normally characterized by *Melaraphe unifasciata* (Plate 2, Fig. 1). During low tides in summer, however, *Melaraphe* migrates downwards, and may be more common among the *Chamaesipho* barnacles of the upper littoral. When this happens mostly bare rock is left in the upper part of the lower supralittoral.

At higher levels, *Melaraphe* seeks shelter in cracks or crevices or around pools, where it occurs in very dense clusters. The banded *Melaraphe praetermissa* (May) may also occur in sheltered places.

A thin black film on the rock in less extreme places is often due to the lichen *Verrucaria.** Where rocks or boulders occur, the isopod *Ligia australiensis* (Dana) is usually found, and in pools or crevices the orange-yellow crab *Leptograpsus variegatus* (Fabricius) may occur.

Littoral zone

The littoral zone, especially under extreme wave action with strong surge up the rock face, is dominated throughout its height by barnacles (Plate 2, Fig. 2). Only in the lower littoral do algae become codominant. In less extreme conditions, or where there is broken rock, algae dominate the lower littoral and gastropods and mussels the mid littoral. On smooth rock faces there is little overlapping of the zones, but more on irregular or broken rocks.

Upper littoral.—On the roughest slopes this is characterized by a well-defined band of the honeycomb barnacle, *Chamaesipho columna* (Spengler) (Plate 3, Fig. 1).

*Probably *V. microsporoides* Nyl, according to the late Mr. P. Bibby.

With less extreme wave action, *Chthamalus antennatus* Darwin is often present slightly above or mixed with the *Chamaesipho*. At an upper littoral level, but in heavy shade under rocks, *Tetraclita purpurascens* (Wood) occurs.

Under hot, dry conditions, *Melaraphe* is often found amongst the upper littoral barnacles. In such cases it is more satisfactory to consider the upper limit of barnacles rather than the lower limit of *Melaraphe* as marking the littoral–supralittoral boundary.

Mid littoral.—On steep, exposed slopes, the surf barnacle *Catophragmus polymerus* Darwin dominates the mid littoral; few other organisms are present (Plate 2, Fig 2). On gentler slopes (e.g. some areas of Point Sinclair), the mussel *Brachyodontes rostratus* (Dunker) occurs in the lower *Catophragmus* zone (or just below), very much as it does along the Victorian coast (Plate 4, Fig. 2) (Bennett and Pope 1953, p. 116). Scattered among the barnacles and mussels, isolated gastropods such as *Patelloida latistrigata* (Angas), *Siphonaria diemenensis* Quoy & Gaimard, and *Neothais textiliosa* (Lamarck) occur. Blue-green algae, mainly *Rivularia firma* Womersley, *Isactis plana* (Harvey) Thuret, and sometimes *Hydrocoleum comoides* (Harvey) Gomont, occur in the lower part of the mid littoral, occasionally extending well up into it. *Polysiphonia* sp. and *Nemalion helminthoides* (Velley) Batters may also be found.

On somewhat less rough coasts the gastropods listed above, together with *Notoacmea septiformis* (Angas), *Patelloida alticostata* (Angas), and *Cellana tramoserica* (Sowerby), may become codominant through the mid littoral, and the serpulid worm *Galeolaria caespitosa* Lamarck becomes prominent in the lowest part of the mid littoral. *Galeolaria* usually occurs as scattered tubes on the rock, and only rarely in local shelter around pools have masses up to 1 cm thick been seen.

Along this type of coastline then, as conditions of roughness become less extreme, the surf barnacle decreases in importance while gastropods and *Galeolaria* become more prominent. The blue-green algae *Rivularia firma* and *Isactis plana* are usually present, but vary greatly in abundance.

On granitic and gneissic rock, in moderately rough places with considerable surge (e.g. Point Sinclair in parts, Point Drummond, and Point Westall), a community of the brown alga *Splachnidium rugosum* (L.) Greville occurs superimposed among the *Catophragmus* (Plate 3, Fig. 2; Plate 4, Fig. 1). The alga may occur as scattered plants, but more often as a fairly dense cover over several square yards, similar to its occurrence on Victorian coasts (Bennett and Pope 1953).

Lower littoral.—In the roughest places this is essentially a *Balanus*–coralline alga association, the presence of the barnacles being indicative of extreme wave action (Plate 5, Fig. 2).

At Point Sinclair, and in areas at Cape Du Couedic and Vivonne Bay (south side of Ellen Point), *Balanus nigrescens* Lamarck is well developed, extending a foot or so above the coralline mat as a fairly pure *Balanus* community (Plate 5, Fig. 1). The coralline algae, mainly *Corallina officinalis* L. or *C. cuvieri* Lamarck, grow as a dense mat up to 3 cm high, covering the barnacles to some extent. In a few localities, such as the roughest parts on Ellen Point, a crustose lithothamnion up to 1 cm thick

replaces *Corallina*. Small patches of thin encrusting lithothamnia are not uncommon in this zone.

In somewhat less rough places, *Balanus* disappears and the lower littoral is dominated by the coralline algae. The lower littoral zone provides the severest conditions of wave action of the intertidal region, and any organism growing there is well adapted to the habitat. Apart from the chitons *Poneroplax albida* (Blainville) and *P. costata* (Blainville), few macroscopic animals occur. Algal species are short and stunted, and include *Laurencia heteroclada* Harvey, *Wrangelia plumosa* Harvey, *Dasyopsis clavigera* Womersley, *Nemastoma feredayae* Harvey, *Centroceras clavulatum* (Agardh) Montagne, and *Gigartina* sp.

Sublittoral fringe zone

The roughness of the sea and the steep rock faces on this type of coast usually prevent thorough studies of the sublittoral fringe zone or deeper regions. The dominant organism, however, is the brown alga *Cystophora intermedia* J. Agardh, which forms a distinct zone from about mean low water down for 4 or 5 ft (Plate 6, Fig. 1). The whole zone is exposed during the suck-back of waves at a very low tide.

Under the *Cystophora* fronds (up to 2 ft long) a coralline mat occurs (mainly *Corallina cuvieri*), forming an almost complete cover on the rock. *Corynophloea cystophorae* J. Agardh is usually epiphytic on the *Cystophora*. In roughest areas other large algae are few, but with slight shelter browns such as *Scytothalia dorycarpa* (Turner) Greville and *Ecklonia radiata* (Turner) J. Agardh appear. Many species of smaller algae may occur, including *Caulerpa brownii* Endlicher and sometimes patches of *Xiphophora chondrophylla* (R. Brown) Montagne. Any bare areas of rock are likely to be covered with thin encrusting lithothamnia.

Animals are not conspicuous in this zone, though the mutton-fish *Haliotis* (*H. roei* Gray, *H. emmae* Reeve, *H. laevigata* Donovan, or *H. improbula* Iredale) and the stalked ascidian *Pyura pachydermatina* (Herdman) var. *gibbosa* Herdman occur. The starfish *Coscinasterias calamaria* (Gray) and *Patiriella calcar* Lamarck, are often found where there is some protection. Crustaceans are always common among the algal mat.

Cystophora intermedia is an indicator species of rough to very rough conditions, and disappears if local shelter occurs. Here other species of *Cystophora*, *C. spartioides* (Turner) J. Agardh, *C. subfarcinata* (Mertens) J. Agardh, *C. paniculata* (Turner) J. Agardh, and *C. siliquosa* J. Agardh dominate the upper sublittoral, extending down well below lowest tide level. This is tending to the sheltered rocky coast type, which is described later.

Pools

Pools at various levels of the intertidal region contain such a variety of micro-habitats and flora and fauna that the main types only are listed briefly. In general, pools at any one level contain organisms which occur at a lower level on sloping rock, except at high littoral and supralittoral levels, where distinctive pool species occur. Some coasts, such as on the south side of Ellen Point, Vivonne Bay, are remarkably rich in rock pools of many types; others such as Point Sinclair have few pools.

Pools at a supralittoral level are subject to great ranges in temperature and salinity. Many have no obvious inhabitants except *Melaraphe* around the edge. Others may have a covering of blue-green algae (*Hydrocoleum* and other genera) or green algae such as *Enteromorpha* and *Chaetomorpha aerea* (Dillwyn) Kützing.

Pools at a littoral level, or large pools higher up, often show dense growth of encrusting lithothamnia (especially at Ellen Point); *Hormosira banksii* (Turner) Decaisne may fringe shallow pools, while a variety of small red algae (*Centroceras* spp., *Ceramium* spp., *Laurencia* spp., *Polysiphonia* spp.) occur. Shaded pools may contain algae normally only found in deep water. Molluscs and *Galeolaria*, typical inhabitants of the mid littoral, are common in shallow littoral pools.

Large pools, subject to water inflow even at low tide, provide good growth conditions for many brown algae—especially *Cystophora* spp., *Ecklonia radiata*, *Myriodesma latifolia* Harvey, *Scytothalia dorycarpa*, *Pachydictyon paniculatum* J. Agardh, and smaller red algae.

(2) *Horizontal Intertidal Rock Platforms*.—Under conditions of strong wave action the coast between the headlands and capes of Palaeozoic rock consists of either horizontal calcareous rock platforms or sandy beaches (Plate 1, Fig. 1). Such rock platforms occur from Sorrento or further east in Victoria along South Australian rough coasts and into Western Australia, where similar platforms are found east of Esperance and on the southern part of the west coast. The western part of the south coast of Western Australia is mainly granitic, with only occasional calcareous platforms.

These rock platforms are characteristic in form and structure. Formed by wave action or possibly by solution (Fairbridge 1950) from calcareous consolidated sand dunes of Recent or Pleistocene age, they present a horizontal surface, with more or less numerous pools or depressions of varying sizes. The surface lies at about mean low water neaps and drops off vertically into deep water. The edge is frequently undercut or dissected. At the rear of the reef, the cliffs are more or less vertical, from 20 to 100 ft high, usually with a wave-cut notch near the base. The rock consists of coarse sand grains cemented together with a calcareous matrix, weathering to a rough surface which is especially pitted and jagged above high tide level. Wave action at the edge of the reef is severe, but as waves pass across the reef conditions moderate. Degree of wave splash at the rear varies with distance from the reef edge and with the height of the tide. These rock platforms have been described in some detail at Pennington Bay on Kangaroo I. (Edmonds 1948; Womersley 1948) and the main features only are summarized here. Variation in the ecology of these reefs in the central and western parts of the South Australian coast is relatively minor, although the very rich algal flora permits considerable chance variation in minor species. Similar reefs form most of the coastline in the south-east of South Australia, but as certain ecological, floristic, and faunistic differences are apparent, their description is left till later in this account.

In general, vertical rock at the rear of the reef (mid and upper littoral and supralittoral) is dominated by animals, while the reef surface and edge is dominated by algae.

Zonation on cliffs at the rear of reefs

Supralittoral zone

This zone begins some distance (4–8 ft) up the vertical cliffs and extends up for 3 – 30 ft depending on wave splash. The dominant organism is *Melaraphe unifasciata*, which occurs as scattered individuals, together with *M. praetermissa* and *Ligia australiensis*. The blue-green algae *Symploca hydnoides* Kützing and *Calothrix fasciculata* (mainly around the Great Australian Bight) are found as scattered patches where there is shade. The lichens *Lichina confinis* (F. Muell.) Agardh (more prominent in local shelter) and occasionally *Verrucaria* may occur, while the crabs *Leptograpsus variegatus* and sometimes *Ozius truncatus* (Milne Edwards) forage for food.

Littoral zone

Upper littoral.—Where wave splash is heavy, the upper littoral is dominated by the barnacles *Chthamalus antennatus* and *Chamaesipho columna*.

At the rear of large reefs, where wave splash is consequently less, barnacles are fewer, while the mollusc community of the mid littoral extends upwards and is co-dominant with the barnacles. If wave splash is relatively slight, few barnacles occur and the molluscs dominate both mid and upper littoral zones, which can then scarcely be separated as distinct zones.

Both *Melaraphe* and *Lichina* often extend down into the upper littoral zone.

Mid littoral.—This is typically a mollusc–*Galeolaria*–blue-green algal zone, ranging from 2 to 6 ft in vertical height (Plate 7, Fig. 1).

At the roughest places *Catophragmus polymerus* does occur, but usually as scattered individuals and never like the dense masses on capes of Palaeozoic rock. With the greater wave splash where it occurs, *Catophragmus* is often at the same height as upper littoral organisms under less wave splash, and above the main mollusc zone.

Molluscs occur through the mid littoral, the commonest being *Austrocochlea odontis* (Wood), *A. rudis* Gray, *A. torri* Cotton & Godfrey, *A. adelaidae* (Philippi), *Cominella lineolata* (Lamarck), *Cellana tramoserica*, *Siphonaria diemenensis*, *Patelloida latistrigata*, *P. alticostata*, *Notoacmea septiformis*, *Chizacmea conoidea* Quoy & Gaimard, *Subninella undulata* (Solander), and *Neothais textiliosa*. Where fallen rocks and more shelter occur, *Melanerita melanotragus* (Smith) and *Bembicium melanostoma* (Gmelin) are common, while *Siphonaria baconi* Reeve inhabits flat and rather level rock.

The serpulid worm *Galeolaria caespitosa* is found throughout the mid littoral, but is best developed in the lower part of the zone. Blue-green algae, mainly *Rivularia firma* and *Isactis plana*, are similarly best developed relatively low in the zone, though *Symploca hydnoides* (Plate 7, Fig. 1) and *Hydrocoleum glutinosum* (Agardh) Gomont occur higher where there is partial shade. Thin encrusting lithothamnia may also be common in the lower mid littoral, and thin mats of *Gelidium pusillum* (Stackhouse) Le Jolis and *Bostrychia simpliciuscula* Harvey or *B. mixta* Hooker & Harvey may be found in heavy shade.

Well-developed communities of the black mussel *Brachyodontes rostratus* occur at a mid littoral level at the rear of some reefs but not on others, e.g. on a reef at the end of Pennington Bay, Kangaroo I., at Sleaford Bay (Plate 6, Fig. 2), and outside Venus Bay on Eyre Peninsula.

Around pools at a mid littoral level, and in moister places, the red anemone *Actinia tenebrosa* Farquhar and the green *Oulactis muscosa* (Drayton) and *Cnidopus verater* (Drayton) may be common. Along the coast of Eyre Peninsula *Oulactis mcmurrichi* (Lager) and *Isanemonia australis* Carlgren occur.

The commonest rock-borers are the sipunculid *Phascolosoma tasmaniense* (Fischer) and an isopod, *Sphaeroma* sp.

Organisms of the reef surface

Lower littoral.—This zone includes the base of the cliffs and any higher areas on the reef surface which are exposed at a very low tide—even though occasional waves (perhaps every 5 or 10 min) will wash over the reef. In vertical height this is a narrow zone of 6–15 in., in contrast to the broader mid littoral.

The dominant organism is the brown alga *Hormosira banksii* (forma *sieberi* (Bory) Harvey), which often forms a pure and dense association over many square yards of higher areas of reefs (Plate 7, Fig. 2). *Notheia anomala* Bailey & Harvey is usually parasitic on the bead-like thallus.

Other prominent algae at the rear of reefs are *Ulva lactuca* L. and *Enteromorpha clathrata* (Roth) J. Agardh, which extend from the lower littoral down into pools, and the brown tufts of *Ectocarpus confervoides* (Roth) Le Jolis (in winter) and *Bachelotia fulvescens* (Schousboe) Bornet (in summer). Each may form a pure community in suitable habitats, especially where waves wash up sloping rock. *Lophosiphonia scopulorum* (Harvey) Womersley is also common, and on the west coast of Eyre Peninsula to at least the head of the Great Australian Bight, *Cladophoropsis herpestica* (Montagne) Howe, basal parts of *Struvea plumosa* Sonder, and *Codium capitulatum* Silva & Womersley are common. These green algae grow under shaded conditions.

Reef communities normally under water.—Near the outer edge of the reefs, communities in which coralline algae are codominant are often developed on slightly higher areas. Such areas are subject to heavy wave action, and are only exposed for a short time between waves at an extremely low tide. The most prominent algae are *Corallina cuvieri* on the rock and *Jania fastigiata* Harvey, growing on *Cystophora subfarcinata; C. paniculata* is also common, and numerous smaller algae, more characteristic of the sublittoral fringe, may enter this *Cystophora*–coralline community (Womersley 1948, p. 157). *Balanus nigrescens* is found as scattered individuals where conditions are very rough.

The most prominent organisms of the reef surface, lying in pools or depressions where they are normally never uncovered, are the fucoid algae *Cystophora subfarcinata, C. siliquosa, C. uvifera* (C. Agardh) J. Agardh, *Cystophyllum muricatum* (Turner) J. Agardh, and *Sargassum decipiens* (R. Brown) J. Agardh. These form a "mixed *Cystophora* complex" (Womersley 1948). Normally most species occur together, though *Cystophora uvifera* and *Cystophyllum muricatum* are more characteristic of

inner calmer parts, where they may form fairly pure communities. *Cystophyllum* is tolerant to partial burial by sand.

The number of species in this complex, which covers a large proportion of the surface of most reefs, is comparatively small. This is probably due to the destructive effects of the moving fronds of the fucoids on germlings of other algae and to the less suitable conditions on hot summer days.

When hot summer days and offshore winds coincide with periods of low tide, both *Hormosira* and the *Cystophora* species may suffer considerable damage. Shallow pools of water on the reefs become sufficiently warm to leach fucoxanthin from the thalli, colouring the water brown. The ends of the fronds lying on the surface are killed and blackened, and whole reefs may be affected in this way.

Several other communities of algae occur on the inner reef surface, two of the commonest being *Jania fastigiata* and *Liagora harveyana* Zeh (often coloured blue-green by epiphytic *Calothrix confervicola* (Roth) Agardh). *Ulva lactuca*, *Cladophora valonioides* Sonder, *Cladosiphon filum* (Harvey) Kylin, *Colpomenia sinuosa* (Roth) Derbes & Solier, *Gracilaria furcellata* Harvey, *Champia obsoleta* Harvey, and *Wrangelia plumosa* are also common. On reefs on the west coast of Eyre Peninsula and towards the head of the Great Australian Bight, encrusting lithothamnia, and often the mutton-fish *Haliotis*, are common (Plate 8, Fig. 1); these reefs are probably always wave-washed.

Blue-green algae sometimes colour large areas of the reefs in shallow water, especially where water streams over ledges at low tide. The chief species are *Rivularia firma* on rock, and *Calothrix confervicola* and *Lyngbya* spp. as epiphytes on larger algae.

A number of animals are associated with the algae which dominate the reef surface. The commonest are the molluscs *Austrocochlea adelaidae*, *Subninella undulata*, *Phasianotrochus bellulus* Dunker, *Zemitrella lincolnensis* Reeve, *Dardanula melanochroma* Tate, *Floraconus anemone* (Lamarck), *Cantharidus pulcherrimus* Wood, and *Phasianella ventricosa* Swainson, and the crustaceans *Naxia tumida* (Dana), *Halicarcinus ovatus* (Stimpson), and *Euidotea peronii* (Milne Edwards). Among the holdfasts of the algae are the polychaetes *Platynereis dumerilii* (Audouin & Milne Edwards) s. sp. *antipoda* Hartman, *Nereis cockburnensis* Augener, *Micronereis halei* Hartman, and the ophiuroid *Amphipholis squamata* (Delle Chiaje). The starfish *Patiriella calcar* occurs on well-washed surfaces.

Sublittoral fringe zone

This includes the edge of the reef, extending down the vertical side for the 2–3 ft uncovered during the suck-back of waves at very low tide.

The dominant alga is *Cystophora intermedia*, with a dense and rich undergrowth of numerous algae. The larger species include *Sargassum bracteolosum* J. Agardh, *Scytothalia dorycarpa*, *Ecklonia radiata*, *Cystophora spartioides*, *C. paniculata*, stunted *C. subfarcinata*, and sometimes *Myriodesma latifolia*. *Corynophloea cystophorae* and sometimes *Dasya urceolata* Harvey are epiphytes on *Cystophora intermedia*. Among the smaller species *Xiphophora chondrophylla* (central and eastern parts of South Australian coastline), *Dictyosphaeria sericea* Harvey, *Codium pomoides* J. Agardh,

Choetomorpha darwinii (Hooker) Kützing on *Ballia scoparia* Harvey, *Perithalia inermis* (R. Brown) J. Agardh (to 18 in. high), *Dasyopsis clavigera*, *Laurencia heteroclada*, *Chrondria* sp., and encrusting lithothamnia may be mentioned; but up to 60 species may be found in a very few square yards of this zone. Womersley (1948, p. 159) gives a comprehensive list for this zone at Pennington Bay, Kangaroo I.

The algae of the sublittoral fringe are so dense that animals are usually hidden under them. *Haliotis roei*, *Subninella torquata* (Gmelin), *Neothais textiliosa*, and *Pyura pachydermatina* var. *gibbosa* are the commonest. Crustaceans are prolific amongst the algae, and polychaetes amongst holdfasts of larger species.

(3) *Sandy Beaches* (*on the Open Coast*).—Long sandy stretches and smaller sandy bays are common along the open coast of South Australia. The coastline which separates the Coorong from the sea in the south-east of the State is a stretch of sand about 120 miles long. The action of the sea on these exposed beaches is usually strong. If the sand is coarse and loose, conditions are inimical to animal life. Where the sand is finer and the beaches firmer more life is found. Macroscopic algae are absent. The localities studied were a part of the Coorong near Goolwa, Vivonne Bay (Kangaroo I.), Sleaford Bay (Eyre Peninsula), and the sandy beach at the head of the Bight. South Australian sandy beaches show similarities, especially in the supralittoral and littoral zones, with those described by Dahl (1953).

Supralittoral zone

The supralittoral is much reduced from that of the rocky coast. It is usually marked by cast-up seaweed and debris. The dominant animal is the amphipod *Talorchestia quadrimana*, which is found amongst the cast-up plant material. If a piece of seaweed containing the animals is shaken they fall onto the sand and quickly bury themselves.

Littoral zone

The upper level of the littoral, especially if the beach is scoured with waves, is usually bare and shows little trace of animal life. A small isopod, *Actaecia pallida* (Nicholas & Barnes), and a small springtail, *Pseudanurida billitonensis* (Schött), are sometimes collected on the moist sand. If dead animals are cast up, the isopod *Cirolana woodjonesi* (Hale) may gather about them. If the beach is smooth and firmer the small wedge bivalve *Amphidesma cuneata* (Lamarck) may be found near the surface at about the mid and low tide level. At Goolwa the cockle *Plebidonax deltoides* (Lamarck) has been collected in the lower littoral and the upper sublittoral on calm days.

Upper sublittoral zone

Very few animals have been found here. Other than the *Plebidonax* the only animal collected is the crab *Ovipales bipustulatus* (Milne Edwards), which is sometimes buried in the sand just below low tide level.

(ii) *Sheltered Coasts of Moderate Wave Action.*—Almost half of the coastline of South Australia is sheltered from strong wave action. Most of the north coast of Kangaroo I. and the gulf coasts, apart from those at the southern end facing south

or west, are subject to waves only 1–3 ft high, with comparatively little force. Frequent calmer periods occur when wave action is slight. The upper parts of the gulfs, consisting mainly of sandy or muddy beach, are discussed later in this paper.

Much of the sheltered rocky coast consists of cliffs of varying height with rocks and boulders, sometimes sloping rock platforms, at the base. The rock is usually of Palaeozoic age, frequently with sandy substratum in 3–12 ft or more of water. Sandy beaches are of common occurrence.

The rock and boulder substratum affords a home for many animals not found along exposed coasts. With calm conditions, the zonation is not so spread out as under strong wave action, and some zones may be limited in vertical extent. Tidal range, however, is greater than on exposed coasts. Water temperatures also show a greater range, being higher in summer and lower in winter, than on exposed coasts.

High air temperatures and low humidity become important on these coasts, particularly in summer when hot days and lack of spray must be limiting factors in the height of intertidal zones. In extreme cases (e.g. at Mangrove Point in Spencer Gulf), although the tide rise is about 10 ft, few organisms occur more than 2 or 3 ft above low tide level; on hot summer days intertidal rock exposed for a few hours may be too hot to touch.

Supralittoral zone

Melaraphe unifasciata is normally dominant, though with a restricted vertical range; in extreme conditions on rocky outcrops in the upper part of Spencer Gulf it may be virtually absent. In most places it is found in nooks and crevices, rarely on the bare face of the rock. *M. praetermissa* and *Ligia australiensis* may also occur, but the crab *Leptograpsus variegatus* is rare. Its niche on the protected coast is taken over (at a lower level) by *Ozius truncatus*, an inhabitant of the littoral zone.

Orange and grey lichens become conspicuous on sheltered coasts, but mostly at a high supralittoral level; so high in fact that they are rarely wet by spray, and can scarcely be considered as "intertidal" organisms.

The black lichen *Lichina confinis* is commonly found in the supralittoral or upper littoral.

Littoral zone

Upper littoral.—The dominant organism is *Chamaesipho columna*, with which may be associated *Chthamalus antennatus* and sometimes *Lepsiella vinosa* (Lamarck). The lichens *Lichina confinis* and *Verrucaria* may occur.

Under extreme conditions of summer heat and great tidal range in the upper gulfs, the upper littoral may be very sparsely populated. Where barnacles do occur their upper limit is well below high tide level.

Mid littoral.—This is a mollusc–*Galeolaria*–blue-green algal zone, with the molluscs and serpulid tubes more plentiful than on other coasts in South Australia. Rocks, boulders, and shaded and sheltered habitats provide favourable conditions for three gastropods in particular: *Melanerita melanotragus*, *Bembicium melanostoma*, and *Austrocochlea concamerata*. Other common molluscs are *Austrocochlea torri*, *Siphonaria diemenensis*, *S. baconi*, *Patelloida alticostata*, *P. latistrigata*, *Cominella lineolata*, *Cellana tramoserica*, *Notoacmea septiformis*, *Subninella undulata*, and

Neothais textiliosa. Many of these gastropods extend upwards or downwards from the normal mid littoral region.

Sometimes the mussel *Modiolus pulex* Lamarck forms a community on horizontal platforms very much as *Brachyodontes rostratus* does on the open coast.

Occasionally, as at Wittelbee Point (south of Ceduna) *Chamaesipho* extends down through the mid littoral, where it is codominant with the molluscs.

Galeolaria caespitosa is best developed along the sheltered coast, as a white band 3–9 in. in vertical height and up to ½ in. thick (Plate 9, Fig. 1). Scattered tubes occur on the rock above this main band, which occupies the lowest part of the mid littoral, giving way abruptly to mat-like algae of the lower littoral. In some cases, especially on the sheltered side of boulders or around pools, two distinct subzones occur—the lower of dense *Galeolaria*, the upper of gastropods (Plate 9, Fig. 1).

The best development of *Galeolaria* in South Australia is on jetty piles where it forms encrusting masses up to an inch or more thick, much as it does in New South Wales (Dakin, Bennett, and Pope 1948). A number of other animals shelter in the thick masses of tubes—*Modiolus pulex*, *Desis crosslandi* Pocock, *Perinereis amblyodonta* (Schmarda), *Kellia australis* Lamarck, *Ibla quadrivalis* Cuvier, and *Leptoplana* sp.

Blue-green algae, principally *Rivularia australis* Harvey, *R. firma*, *R. atra* Roth, *Isactis plana*, and *Brachytrichia quoyi* (Agardh) Bornet & Flahault are rather variable in occurrence. Brown crusts of *Ralfsia* sp. are common in the lower part of the mid littoral. *Enteromorpha* spp. may be plentiful, especially in depressions and in pools.

Lower littoral.—In contrast with the higher intertidal levels, the lower littoral is dominated by algae. With moderate wave action, a *Corallina* mat is dominant, but mostly on this type of coast the algal mat varies from mixed *Corallina* and *Gelidium pusillum* to pure *Gelidium*. These algae form a mat or turf up to 1 in. thick, completely covering the rock, and some 6–15 in. in vertical height. *Gelidium pusillum* tends to occur higher than the *Corallina*, particularly if shaded, and may be pure in the upper part of the lower littoral though mixed with *Corallina* below. On rock platforms (as at the Port Willunga–Aldinga reef) two lower littoral associations are prominent; *Gelidium pusillum* in a dense yellow-brown mat, and at a slightly lower level, where slight pools are left at low tide, *Hormosira banksii*.

Brown crusts of *Ralfsia* are also common in the lower littoral, while *Colpomenia sinuosa* is common on rock or on other algae. *Ulva lactuca* and *Cladostephus verticillatus* (Lightfoot) Agardh may extend up into the lower littoral.

Large animals are few, owing to the density of the algal covering, but the chitons *Poneroplax albida* and *P. costata* occur in small numbers. Crustaceans and polychaetes are common in the algal mat, as they are at lower levels.

Upper sublittoral zone

The dominant algae of this zone extend from about low water neaps down for several feet (up to 10 or 12) to well below extreme low tide. The term "sublittoral fringe" is therefore not applied to this zone.

Brown algae, up to 3 or 4 ft in length, are dominant (Plate 9, Fig. 2). The laminarian *Ecklonia radiata* is usually present, together with *Cystophora subfarcinata*, *C. polycystidea* Areschoug, *C. spartioides*, *C. retorta* (Mertens) J. Agardh, *Scaberia*

agardhii Greville, *Sargassum lacerifolium* (Turner) Agardh, and *S. decipiens*. *Cystophyllum muricatum* and *Cladostephus verticillatus* are common in shallow water, and *Ectocarpus* spp. and blue-green algae (especially *Hydrocoleum glutinosum*) are common epiphytes. Other common species are *Caulerpa brownii*, *Dictyota* spp., *Pachydictyon paniculatum*, *Amphiroa anceps* (Lamarck) Decaisne, *Corallina cuvierii*, *Metagoniolithon charoides* (Lamouroux) Weber van Bosse, *Cheilosporum elegans* (Hooker & Harvey) Areschoug, encrusting lithothamnia and other red algae (*Hildenbrandtia*, *Cruoria*), *Pterocladia capillacea* (Gmelin) Bornet & Thuret, and *Laurencia majuscula* (Harvey) Lucas.

A considerable variety of animal life is found in the upper sublittoral, especially where rocks lying in sand provide suitable habitats for many species not found on the upper side of rocks. The following are common: *Haliotis roei*, *H. emmae*, *H. improbula*, the echinoderms *Patiriella gunnii* (Gray), *P. brevispina* H. L. Clark, *P. exigua* Lamarck, *Coscinasterias colamaria*, *Heliocidaris erythrogramma* (Valenciennes), *Petricia vernicina* (Lamarck), and *Tosia australis* (Gray).

Around the base of rocks, under them or in the sand, occur the anemones *Oulactis muscosa*, *Actinia tenebrosa*, *Isanemonia australis*, *Anthothoe albocincta* (Stuckey), and *Anthopleura aureo-radiata* (Stuckey).

Common polychaetes are *Idanthyrsus pennatus* (Peters), *Eunice aphrodite* (Palliser), *E. australis* Quatrefages, *Thelepus plagiostoma* (Schmarda), *Glycera americana* Leidy, *Thormora versicolor* (Ehlers), *Nereis cockburnensis*, *Lepidonotus melanogrammus* Haswell; the crustacea *Helice haswellianus* (Whitelegge), *Halicarcinus ovatus*, *Ozius truncatus*, *Cyclograpsus audouinii* (Milne Edwards), *Crangon villosus* (Olivier); the echinoderms *Nectria multispina* H. L. Clark, *Uniophora multispina* H. L. Clark, *Placophiothrix spongicola* (Stimpson), *Ophionereis schayeri* (Müller & Troschel), *Heliocidaris erythrogramma*, *Amblypneustes ovum* (Lamarck); and several sponges and ascidians are found.

Where rock gives way to a sandy bottom the marine angiosperms *Zostera muelleri* Irmisch and (in 2 ft or more of water) *Posidonia australis* Hooker f. are common. The *Posidonia* leaves bear numerous epiphytes, particularly *Pachydictyon fucellatum* (Harvey) J. Agardh, *Asperococus bullosus* Lamouroux, *Colpomenia sinuosa*, and *Ceramium puberulum* Sonder.

(*b*) *Coasts of Slight Wave Action, with Sandy or Muddy Flats or Beaches*

This type of habitat includes a number of semi-enclosed or almost land-locked bays on the coast of Eyre Peninsula and the north coast of Kangaroo I., and much of the upper parts of Spencer and St. Vincent Gulfs, particularly the western shores. Wave action is very much reduced compared with coasts previously discussed. Much of the time it is negligible, and only where wind blows across larger areas of deeper water is wave action appreciable. In such cases, fragments of the sheltered rocky coast type of habitat may occur within otherwise calmer areas. In many cases conditions grade from sheltered rocky coasts to calm tidal flats, though at the entrance of many bays the transition covers a relatively short distance.

Typically the shore topography comprises very gently shelving flats above and below low tide level, descending gradually into deeper water or (especially in inlets)

abruptly to a central channel 2 fm or more deep (Plate 10, Fig. 2). The littoral region may rise gently to a sandy beach or low cliffs. Boulders may occur at or above high tide level. This gentle shelving of the intertidal region often results in grading between zones.

The composition of the substratum varies considerably. Apart from rocks or cliffs at high levels, most of the littoral consists of sand, mud, or usually a mixture of the two. Frequently higher levels are sandier than lower ones, and the sublittoral is usually mud. Mud flats are usually calmer than sandy areas. Some of the areas studied were the Cockle Bank in Eastern Cove, Kangaroo I., Coffin Bay, and Outer Harbour, which are chiefly sandy; Proper Bay, Venus Bay, and Streaky Bay on Eyre Peninsula, which are intermixed sand and mud; and American River inlet on Kangaroo I., which is chiefly mud. In the latter and similar localities, the mud is up to 10 in. deep, and often overlain by a thin layer of sand.

The amount of plant life on sandy and muddy shores varies considerably. On sand flats only a few species of small algae occur attached to cockle or other shells in the lower littoral and sublittoral zones. The flora of muddy areas is greater, for here the more stable substratum supports extensive beds of marine angiosperms such as *Zostera* and *Posidonia*, and firmly embedded molluscs (living or dead) provide a foothold for larger algae. Examples of the latter are *Hormosira* on *Brachyodontes erosus* in the lower littoral, and an occasional fucoid alga on molluscs in the sublittoral. Extremely few algae can grow directly in the mud or sand.

Most of the animals which are inhabitants of sand and mud flats are able to avoid their enemies and the hazards of desiccation by burrowing. Sand, on account of its tendency to shift, is not a good medium in which to form permanent burrows. Sand flats also tend to dry out more quickly than mud flats owing to the lower water-holding capacity of sand and the generally steeper slope of sandy shores. Consequently, as pointed out by Yonge (1953), animals which live in mud flats do not have to burrow as deeply as those which live on sandy shores.

Distinguishing features of this type of coast, apart from its topography, are the virtual absence of *Melaraphe* and barnacles (except *Elminius modestus* Darwin on jetty piles), the dominance in most localities of the small form of *Bembicium melanostoma* in the mid littoral, the presence of the forma *labillardieri* (Bory) Harvey of *Hormosira banksii*, the virtual absence of large brown algae (Fucales and *Ecklonia*) from the upper sublittoral, and the presence of extensive areas of the marine angiosperms *Zostera* and *Posidonia*.

A detailed account of the ecology (with algal emphasis) of American River inlet is given by Womersley (1956).

Supralittoral zone

The supralittoral may consist of:

(1) A bare zone of loose or compacted sand of varying degrees of coarseness, or of a mass of broken shells. Few organisms occur here, apart from *Talorchestia quadrimana* (Haswell) amongst cast-up plant debris.

(2) Low rocky cliffs, such as in parts of American River inlet, which are generally bare apart from rare occurrences of the green alga *Gayella*

polyrhiza Rosenvinge (Womersley 1956, p. 77). If wave splash occurs then *Melaraphe unifasciata* is present in small numbers, together with *Ligia australiensis*.

(3) Low swampy areas with a muddy substratum which extends up through the supralittoral; samphires are prominent, forming a dense cover (see below, under "upper littoral").

Littoral zone

Upper littoral.—Substrata in the upper littoral are similar to those listed above for the supralittoral. Most prominent are the samphires where the substratum is muddy and a few inches or more deep. These include three species of Chenopodiaceae, *Salicornia australis* Banks & Solander, *Arthrocnemum arbuscula* (R. Brown) Moquin-Tandon and *Kochia oppositifolia* F. Muell.; other species may occur. They occur in that order from below upwards, with considerable mixture. *Salicornia* forms low spreading mats up to 6 or 8 in. high, while the others reach 3–5 ft in height. Under the bushes algal mats of *Gelidium pusillum*, *Bostrychia simpliciuscula*, and occasionally *Chaetomorpha capillaris* (Kützing) Boergesen have been found. *Bembicium melanostoma* is also common here.

On firm mud or rock, where samphires do not occur, the gastropod *Bembicium melanostoma* is the dominant organism, though less common than in the mid littoral. Mats of *Gelidium pusillum* and *Bostrychia simpliciuscula* (sometimes also *B. mixta*) occur in shaded parts at the base of cliffs or under rocks.

In the upper gulfs and in parts of Denial Bay, the mangrove *Avicennia marina* (Forster) Vierhapper var. *resinifera* (Forster) Bakhuizen van den Brink is common, forming moderately extensive thickets of trees up to 20 ft high. It extends from below high tide level to somewhat above low tide. The mud between the trees is fairly bare, though mats of *Enteromorpha* occur, and the barnacle *Eliminius modestus* and serpulid *Galeolaria caespitosa* occur on the pneumatophores and lower trunks. Brown films on exposed mud are common, due to diatoms and blue-green algae.

Barnacles are only found in the upper littoral where there is local wave wash and rocky outcrops, or on piles and stakes in the water. The chief form is *Eliminius modestus*.

Mid littoral.—The two most important organisms here are the mussel *Modiolus inconstans* (Dunker) and the gastropod *Bembicium melanostoma*. Either may be dominant, and often they are codominant. *M. inconstans* forms extensive beds in some areas (Cockle Bank, Eastern Cove) and affords shelter for a number of other animals including the small bivalve *Kellia australis*, the polychaete *Perinereis amblyodonta*, the barnacle *Ibla quadrivalis*, and the sipunculid *Phascolosoma tasmaniense*.

Thick masses of *Galeolaria caespitosa* often occur in the mid littoral, while other common molluscs are *Siphonaria diemenensis*, *Melanerita melanotragus*, and *Cominella lineolata*. The crab *Helice haswellianus* occupies the niche of *Ozius truncatus* on other coasts.

On sand flats the mid littoral is often a bare zone, though the gastropod *Salinator fragilis* (Lamarck) may occur.

In the upper gulfs *Avicennia* is often dominant in the mid littoral (see "upper littoral" above).

Few algae occur in this zone. Mats of *Enteromorpha* are occasionally found, and the blue-green algae, *Isactis plana*, *Rivularia nitida* Agardh, and others may occur though they are not conspicuous.

Lower littoral.—Where the substratum is fairly pure, deep sand, the dominant organisms are the cockles *Katelysia scalarina* (Lamarck) and *K. peronii* (Lamarck), which occur below the surface. They extend down into the sublittoral and commonly bear a plant of *Enteromorpha clathrata*.

If the substratum contains much mud, the razor shell *Pinna dolabrata* Lamarck is dominant (e.g. Outer Harbour and Streaky Bay) (Plate 10, Fig. 2), but if the mud layer is thinner *Brachyodontes erosus* (Lamarck) is common and may form extensive beds (Plate 10, Fig. 1).

Commonly growing on rock, on pebbles, or on *B. erosus* is the fucoid alga *Hormosira banksii* f. *labillardieri*, which frequently dominates and distinguishes the lower littoral zone in calm muddy bays or inlets. At the same level or slightly higher mats of *Chaetomorpha billardieri* Kützing may be common, while stunted fragments of *Corallina* also occur.

In some areas, such as at Outer Harbour and on the Cockle Bank, Eastern Cove, the burrowing anemone *Edwardsia australis* Carlgren is dominant over large areas of the sand flats at a lower littoral level. Where sand and mud are intermixed the polychaete *Arenicola assimilis affinis* Ashworth is common. Yonge (1953) states that in the northern hemisphere the presence of *A. marina* indicates the beginning of the transition from sand to mud. This is also true of *A. assimilis affinis* in South Australia. Along the mud and sand banks of channels in the lower littoral the large polychaete *Eunice tubifex* Crossland may be dominant.

On mud flats where sand is almost absent *Edwardsia* and *Arenicola* do not occur. Three terebellid polychaetes, however, become very common over large areas, *Eupolymia trigonostoma* Schmarda, *Terebella haplochaeta* Ehlers, and *Thelepus plagiostoma* (Schmarda). They occur under dead shells and rock fragments or in the mud itself.

The oyster *Ostrea sinuata* Lamarck is frequently found attached to the shells of *Pinna*. This oyster does not in South Australia form the distinct "oyster zone" of the New South Wales (Dakin, Bennett, and Pope 1948) and Queensland coasts (Endean, Kenny, and Stephenson 1956).

Animals extending from the lower littoral up into the mid littoral

MOLLUSCA: *Austrocochlea zebra* (Menke) (wide-ranging), *Cominella lineolata*, *Zeacumantis diemenensis* Quoy & Gaimard, *Anapella pinguis* (Crossland & Fischer), *Philene angasi* (Crossland), *Mactra pura* Deshayes, *Uber conicum* Lamarck (in sand), *Cardium racketti* Donovan, *Soletellina biradiata* Wood, *Fasciolaria australasia* Perry, *Vicimitra glabra* (Swainson), *Parcanassa pauperata* (Lamarck), *Niotha pyrrhus* Menke, *Ischnochiton lineolatus* (Blainville) (under stones and dead shells), and *I. cariosus* Pilsbry.

CRUSTACEA: *Helice haswellianus* ("mud crab"—mid and upper littoral), *Philyra laevis* (Bell) ("pebble crab"), *Callianassa ceramica* (Fulton & Greville), *Crangon villosus*.

POLYCHAETA (mainly lower littoral and upper sublittoral): *Eunice aphrodite*, *E. australis*, *Lepidasthenia michaelseni* (Augener) (commensal with Eunicidae), *Thormora versicolor*, *Perinereis amblyodonta*, *Glycera americana*, *Chaetopterus variopedatus* Renier, *Branchiomma cingulata* (Grube), *Clymenella insecta* Ehlers, and *Ceratocephalus edmondsi* Hartman.

HOLOTHURIAN: *Leptosynapta dolabifera* (Stimpson), and *Mensamaria thomsoni* (Hutton).

Sublittoral zone

Sublittoral fringe.—Below low tide level plant life is dominant, except in very sandy areas which harbour animals below the surface; the animals found in the lower littoral may occur here.

In muddy areas, growing on pebbles and shells, and sometimes loose-lying, are numerous algae forming a rather mixed zone, dominated by *Hypnea musciformis* (Wulfen) Lamouroux and *Spyridia biannulata* J. Agardh. Other common algae are *Centroceras clavulatum*, *Ulva lactuca*, *Enteromorpha clathrata*, *Cladophora fascicularis* (Metens) Kützing, *Acetabularia peniculus* (R. Brown) Solms-Laubach, and lithothamnia. Others are listed by Womersley (1956, pp. 80–1).

Animals usually found amongst the algae are the echinoderms *Patiriella exigua*, *P. gunnii*, and *Tosia australis*, the isopod *Eudotea peronii*, and small fish of the families Syngnathidae and Blenniidae.

Upper sublittoral.—Here the marine angiosperms *Zostera* and *Posidonia* become dominant and cover wide areas. *Zostera muelleri* extends from the lower littoral downwards. Above low tide level it is short and poorly developed, usually in moister depressions. Below low tide it forms a dense sward, up to 12 in. high, extending downwards for several feet. Owing to the smooth leaves, epiphytes on *Zostera* are few.

Posidonia australis occurs from a foot or so below low tide into several fathoms (about 5–6) of water, forming a dense association. At very low tide the stiff leaves just project above the water, giving a characteristic appearance to the area (Plate 11, Fig. 1). *Posidonia* bears a wealth of epiphytes on its rough leaves (see Womersley 1956, p. 82).

The angiosperm *Halophila ovalis* (R. Brown) Hooker f. is also common in deeper areas (4 ft or more below low tide), particularly on the edges and sides of channels.

Large fucoid algae are virtually absent from the upper sublittoral. Occasionally *Cystophyllum muricatum* and *Cystophora cephalornithos* (Labilliardiere) J. Agardh occur in local tidal currents or under slight wave action. The absence of these fucoid algae, and dominance of *Zostera* and *Posidonia* in the upper sublittoral, are distinguishing features of this type of habitat.

The starfish *Coscinasterias calamaria*, *Uniophora multispina*, and *Petricia vernicina*, the ophiuroids *Placophiothrix spongicola* and *Ophionereis schayeri*, colonial

ascidians (*Austrobotryllus* spp.), and yellow and purple sponges are common in the upper sublittoral.

B. THE SOUTH-EASTERN COAST

The coast from Robe eastwards to the Victorian border consists of calcareous sand-rock cliffs and platforms of Pleistocene to Oligocene Age with interspersed sandy beaches. No outcrops of older rocks are indicated on the geological map of South Australia. Small islands lying a short distance offshore are common.

The topography, substratum, and conditions of wave action are similar to those described in Section IVA(i)(2). Water temperature is, however, somewhat lower, ranging from 13 to 17°C (see Figs. 2(*a*) and 2(*b*)). The coast at Robe has been examined more frequently than the coast further east.

Supralittoral zone

Melaraphe unifasciata is dominant over much of the supralittoral, though on rock exposed to continuous sun the lichens *Lichina confinis* (Plate 11, Fig. 2) and *Verrucaria* become dominant. These lichens are generally more conspicuous on the south-east coast than on the central and west coasts of South Australia. Some specimens of the banded *Melaraphe praetermissa* have been collected, and *Ligia australiensis* is always plentiful. *Calothrix* sp. may be common in some places.

Littoral zone

Upper and mid littoral.—One of the most conspicious features of the south-east coast of South Australia is the almost complete absence of barnacles in the upper and mid littoral zones. Only isolated specimens of *Chthamalus antennatus* and *Chamaesipho columna* have been observed, and no *Catophragmus* where it might have been expected. Barnacles are virtually absent from the jetty piles at Robe and Beachport, a very rare occurrence in South Australia. Bennett and Pope (1953, p. 120) also report a reduction of the barnacle zone along the western shores of Victoria.

Consequently the upper littoral is often a sparsely populated zone, though molluscs from the mid littoral extend up through it. Usually upper and mid littoral zones cannot be distinguished.

Molluscs and *Galeolaria* dominate the mid (and upper) littoral zone, though often less dense than on other coasts (Plate 12, Fig. 1). *Galeolaria caespitosa* occurs only as scattered tubes on the rock. The chief molluscs are *Cellana tramoserica*, *Patelloida alticostata*, *Siphonaria diemenensis*, *S. baconi*, *Notoacmea septiformis*, *Austrocochlea adelaidae*, *A. torri*, *A. concamerata* (Wood), *Melanerita melanotragus*, *Subninella undulata*, *Neothais textiliosa*, and *Bembicium melanostoma*. There is no essential difference between this mollusc population and that of the mid littoral on rock platforms of the central and west coasts of South Australia.

The extensive beds of *Brachyodontes rostratus*, typical of much of the Victorian coast (Bennett and Pope 1953) do not occur at any of the localities studied on the south-east coast of South Australia, except on the foreshore breakwater at Robe. Here *B. rostratus* forms well-developed beds in the mid littoral.

Algae are not prominent in the mid littoral. *Porphyra columbina* Montagne, with some *P. umbilicalis* (L.) J. Agardh, is plentiful in suitable habitats during winter months. *Scytosiphon lomentarius* (Lyngbye) J. Agardh is also a winter species. Patches of *Gelidium pusillum* occur in shaded areas, but blue-green algae are not so conspicuous.

Within Guichen Bay, on the foreshore breakwater, *Enteromorpha* (*compressa?*) and *Ectocarpus confervoides* occur in the upper littoral during winter.

Lower littoral.—The reef surface in the lower littoral is dominated by *Hormosira banksii* (f. *sieberi*) and is very similar to comparable reefs on central and western coasts. The chitons *Poneroplax albida* and *P. costata* are the most prominent animals, though mid littoral molluscs often move down to this zone. On the breakwater near Robe *Corallina* sp. together with tufts of *Centroceras clavulatum* and *Griffithsia* sp. dominate the lower littoral.

Upper sublittoral zone

Pools at the rear of reefs contain many of the species found on other comparable reefs, but a few of cooler-water affinities appear as well—*Myriogloia sciurus* (Harvey) Kuckuck, *Eudesme harveyana* Kylin (these two are winter forms), *Codium fragile* (Suringar) Hariot, *Grateloupia* sp., and *Pleonosporium comatum* (J. Agardh) De Toni. *Cystophora intermedia*, so characteristic of the sublittoral fringe on other coasts of South Australia, is here largely replaced by the giant fucoid *Durvillea* (*Sarcophycus*) *potatorum* Areschoug. *C. intermedia* is sometimes found but is not prominent. In deeper reef pools, with some protection, *Durvillea* disappears and species of *Cystophora* and *Sargassum* become dominant. The species of these two genera are much the same as on coasts to the west.

In deeper water, the kelp *Macrocystis angustifolia* Bory* is often dominant, rising from a few fathoms of water to the surface. It does not occur off the most exposed points, and within Guichen Bay grows just below low tide level (Plate 12, Fig. 2).

The animals of the sublittoral have not been extensively studied. *Haliotis laevigata* and *H. improbula* are amongst the commonest.

V. The Relationships of the South Australian Intertidal Flora and Fauna

(*a*) *Differences between the South-Eastern and Central-Western Parts of the South Australian Coast*

The south-eastern coast, consisting chiefly of rock platforms subject to strong wave action, differs from similar coasts further west in the following respects:

(1) Barnacles are virtually absent in the upper and mid littoral zones, which are populated mainly by molluscs.

(2) *Porphyra* (mainly *P. columbina*) is prominent in the mid littoral during winter, while it is of sporadic occurrence on coasts further west.

(3) The giant brown algae *Durvillea potatorum* and *Macrocystis angustifolia* are prominent below low water level.

*Incorrectly given by Bennett and Pope (1953) as *M. integrifolia.*

(4) Some algal species are limited to the slightly cooler water of the south-eastern coasts.

The reduction in numbers of barnacles has also been recorded by Bennett and Pope (1953) for western Victorian coasts. Further east in Victoria barnacles reappear. There is no satisfactory explanation as yet for this.

The most important difference is the presence of *Durvillea* and *Macrocystis*, though outlier patches of *Macrocystis* may occur further west (Womersley 1954*a*).

These differences separate the south-east coasts from the rest of South Australia, but they are relatively minor compared with the many features in common.

(*b*) *A Note on Biogeographical Provinces*

The present authors agree with Bennett and Pope and others that the organisms on open coasts are the best indicators of biogeographical provinces, since they are not exposed to the environmental (especially temperature) fluctuations of inhabitants of inlets and estuaries. This does not mean, however, that ecological studies on calmer coasts should be neglected. Comparisons between similar environments are usually justified. It is comparisons between calm inlets and exposed coasts which must be made with caution, since some species can extend their range under sheltered conditions.

This study, as were those of Bennett and Pope (1953) on the Victorian coast, Dakin, Bennett, and Pope (1948) on the New South Wales Coast, and Endean, Kenny, and Stephenson (1956) on the Queensland coast, is based on the ecology and distribution of the common intertidal organisms. In discussing biogeographical provinces it must be remembered that other aspects (such as broader floristic and faunistic relationships, including all organisms, common or rare) are also involved, and should be taken into account. In many animal groups the required data are not yet available.

(*c*) *Ecological Comparison of South Australian Coasts with Coasts Elsewhere*

(i) *Comparison with Victorian Coasts.*—Bennett and Pope (1953) give the only account of the intertidal ecology of Victorian coasts.

Supralittoral zone

This zone is essentially the same in both States, with *Melaraphe unifasciata* and *M. praetermissa* dominant and *Ligia australiensis* common. *M. unifasciata* is the commonest littorinid in South Australia. The lichens *Lichina confinis* and *Verrucaria* occur. No *Nodilittorina* or *Tectarius*, characteristic of the New South Wales and Western Australian coasts respectively, are found in South Australia.

Littoral zone

Upper littoral.—This is essentially a barnacle zone, occupying the same shore levels in both States; *Chthamalus antennatus* and *Chamaesipho columna* are found at least as far west as the head of the Great Australian Bight. An area where barnacles are virtually absent occurs in the south-east of South Australia and in western Victoria. No reason for this is apparent, as all the barnacles (except *Balanus*

nigrescens) occur in Tasmania (Guiler 1955, p. 145). *Eliminius simplex* Darwin and *E. modestus* are found in calmer parts of the South Australian and Tasmanian coasts, and *E. modestus* is recorded by Bennett and Pope from Victoria.

Mid littoral.—The mollusc–*Galeolaria*–blue-green algal zone is a feature of both States. The blue-black mussels *Brachyodontes rostratus* and *Modiolus pulex* are common in South Australia at least as far west as Point Sinclair. They never, however, cover such extensive areas as those in Victoria (Bennett and Pope 1953, Plate 4, Fig. 1), or Tasmania (Guiler 1954, Plate 1, Fig. 1). Seven of the nine bivalves listed by Bennett and Pope occur in South Australia. In rough places the surf barnacle *Catophragmus polymerus* is prominent, extending west at least as far as the head of the Great Australian Bight. In suitable habitats it completely dominates large areas. *Tetraclita purpurascens* extends through Victoria, South Australia, and the south coast of Western Australia.

Most of the gastropods of the exposed South Australian coast extend as far as Sorrento in Victoria, and of 47 species listed for the whole Victorian coast, 29 (62 per cent.) occur in South Australia. Of 11 chitons of the Victorian coast, six occur in South Australia, and *Poneroplax albida* and *P. costata* are the commonest along the exposed coasts of the two States.

Galeoaria caespitosa is prominent as far west as Eucla, but is best developed in sheltered localities. The brown alga *Splachnidium rugosum* is common in suitable habitats in both States, while *Porphyra* in winter is more conspicuous from Robe eastwards.

Lower littoral.—This zone is essentially similar in both States, being occupied by a "coralline mat" or "algal turf" (Bennett and Pope 1953), with *Poneroplax* chitons prominent on bare rock at or just below this level. On very rough areas *Balanus nigrescens* is prominent. On rock platforms at a low littoral level *Hormosira banksii* forms a distinct association, with *Notheia anomala* as its chief epiphyte in exposed localities. The "bare" zone described by Bennett and Pope (1953, p. 121) for Victoria, where chitons are common, is usually covered in South Australia with thin encrusting lithothamnia or other small algae. *Pyura stolonifera* (Heller) is absent in South Australia except on the piles of a few jetties.

Upper sublittoral or sublittoral fringe zone

Here the major difference between the Victorian coast and the central–western parts of the South Australian coast is found. In the latter areas, this zone is dominated by species of *Cystophora*, particularly *C. intermedia* under rough conditions. From Robe eastwards (to Bermagui in New South Wales) and also in Tasmania the giant fucoid *Durvillea* (*Sarcophycus*) *potatorum* is dominant from above low water level down for some feet, in conditions of strong wave action. Under slightly calmer conditions *Cystophora* spp. or *Phyllospora comosa* (Labilliardiere) Agardh become dominant, and *C. intermedia* has been recorded from some parts of the Victorian coast (e.g. Wilson's Promontory). In deeper water the kelp *Macrocystis angustifolia* occurs, the tops of the fronds floating on the surface. *Ecklonia radiata* is of scattered occurrence but fairly common on exposed coasts in both States. Only on sheltered rocky coasts, however, does it become dominant.

Associated algae of this zone are similar in both States. There is, however, a small element of Victorian species which are not found in South Australia (e.g. *Cystophora torulosa* (R. Brown) J. Agardh).

Of the other animal groups listed by Bennett and Pope (1953, pp. 127–34) for Victorian coasts, 13 of 17 echinoderms, 20 of 25 arthropods, 2 of 4 ascidians, and 5 (at least) of 8 polychaetes are known from South Australia. South Australian sponges and Bryozoa are not sufficiently well known to make comparisons.

Bennett and Pope (1953, p. 147) list 16 species of animals which they claim "characterize" the cool temperate region (i.e. the Victorian and Tasmanian coasts). Of these, 10 are well known in South Australia, viz. *Melaraphe praetermissa*, *Lepsiella vinosa*, *Cominella lineolata*, *Siphonaria diemenensis*, *Tosia australis*, *Nectria ocellata*, *Patiriella brevispina*, *Mensamaria thomsoni*, *Brachynotus octodentatus* (Milne Edwards), and *Lomis hirta* (Milne Edwards), and an eleventh, *Austropromia polypora* (Clark), which they state is "rarer", is recorded by Clark (1946, p. 114) as extending from Tasmania to Rottnest I.

Of some 93 algae listed by Bennett and Pope for the Victorian intertidal zone, 15 are unidentified and nine are from the "wrack". It is likely that further collecting would show many algal species to be present where not recorded by Bennett and Pope. Of the 78 named algae, 10 are cosmopolitan, 53 are widely distributed along southern Australia and Tasmania, and 15 are limited to Victorian and Tasmanian coasts or the eastern part of South Australia. Thus 63 of 78 species are common to both States. This does not support the view that Victorian coasts should be separated as a distinct province from South Australian coasts.

(ii) *Comparison with Tasmanian Coasts.*—Bennett and Pope (1953) considered that most of the Tasmanian coastline is allied to the Victorian, with the probability of a "truly cool-temperate region" in southern Tasmania. The south-eastern Tasmanian chitons were considered by Iredale and May (1916) sufficiently distinct from those of the north coast to designate the east coast of Tasmania as the Maugean Region (Province). The north coast chiton fauna was considered to be "practically pure Adelaidean, but with a slight Tasmanian element". Bennett and Pope (p. 153), however, believe that these differences were a "mere accentuation of the differences . . . already evident on the Victorian coast", and they extend the Maugean Province to include the whole coast of Tasmania and that of Victoria. Guiler (1952*b*, 1954) supports this view of the close affinities between Tasmanian and Victorian coasts. He points out, however, that *Balanus nigrescens* is absent in Tasmania (Guiler 1955).

Ashby (1926) recognized a "Tasmanian region" on the basis of chiton distribution, since there are a "sufficient number of species that are peculiar to Tasmania".

The accounts of Guiler and of Cribb (1954), and algal collections of Miss I. Bennett from a number of exposed localities around northern Tasmania (determined by H. B. S. Womersley) show that apart from *Lessonia corrugata* Lucas, *Xiphophora gladiata* (Labilliardiere) Montagne (=*billardieri*) and *Adenocystis utricularis* (Bory) Skottsberg the prominent algae of the intertidal zone are very similar to those of Victoria, and the majority of them are also found on South Australian coasts.

Guiler (1954) lists common intertidal animal species of the Tasmanian coast. Of 65 listed for the north coast, 43 are well known in South Australia; for the west coast, 39 of 55; for the south coast, 90 of 147; and for the east coast, 73 of 122.

(iii) *Comparison with the South Coast of Western Australia.*—Little information is available on the intertidal region of the Western Australian coast. The following brief notes are based largely on a survey of the south coast made by Miss E. Wollaston, Department of Botany, University of Adelaide, during January–February 1957. Macpherson (1954) gives a list of the molluscs of the Recherche Archipelago, and certain mollusc records have been made available by Mr. B. C. Cotton of the South Australian Museum. Mrs. L. Marsh, Department of Zoology, University of Western Australia, has also confirmed distribution records along this coast.

The present authors are in no way attempting here to give an account of the intertidal organisms of the south coast of Western Australia. A few important differences only from South Australian coasts will be mentioned.

Little information is available on the coast between Eucla and Israelite Bay, a distance of over 300 miles. The Admiralty Chart and Vol. 1 of the "Australia Pilot" indicate that this coast probably consists of long stretches of sandy beach, with only isolated rocky outcrops except, perhaps, between Eyre and Point Culver.

From near Israelite Bay westwards, granitic points and outcrops occur, with interspersed areas of Tertiary limestone giving intertidal platforms similar to the calcareous sand-rock platforms in South Australia.

Supralittoral zone

Melaraphe unifasciata and *M. praetermissa* are well known on the south and south-west coasts, and blue-green algae (*Calothrix*) are a feature of the high supralittoral on granite points. *Tectarius rugosus* (Menke) occurs at Cape Leeuwin and at Albany, but was not collected at Esperance. The supralittoral thus differs from that in South Australia in the presence of *Tectarius* in the far west.

Littoral zone

A striking difference from South Australian coasts appears to be the absence of barnacles in the upper and mid littoral zones. No *Chthamalus*, *Chamaesipho*, or *Catophragmus* were seen by Miss Wollaston anywhere on the south coast, though in the lower littoral *Balanus nigrescens* is often prominent and *Tetraclita purpurascens* occurs in its normal habitat. The mussel *Brachyodontes rostratus* is also apparently absent. Macpherson (1954) remarks on the absence of this bivalve from the Recherche Archipelago.

Many of the South Australian mid-littoral molluscs occur in the west. The following were collected at Esperance: *Siphonaria baconi*, *Notoacmea septiformis*, *Patelloida alticostata*, *Bembicium melanostoma*, *Melanerita melanotragus*, *Austrocochlea concamerata*, *A. adelaidae*, *A. zebra*, *A. torri*, *A. rudis*, and *Subninella torquata*. Notable absentees were *Cellana tramoserica*, *Neothais textiliosa*, and *Siphonaria diemenensis*, while species found only in Western Australia include *Dicathais aegrota* (Reeve) and *Siphonaria luzonica*.

Of some 159 species listed by Macpherson (1954) for the Recherche Archipelago, 113 occur in South Australia.

Galeolaria caespitosa occurs along the south coast of Western Australia, but apparently disappears somewhere north of Dunsborough (near Cape Naturaliste) on the west coast.

The lower littoral is similar to the corresponding zone in South Australia, the most noteworthy change being the disappearance of *Hormosira banksii* west of Albany. *Poneroplax albida* and the Western Australian *Clavarizona hirtosa* (Blainville) were the main chitons collected at Esperance.

Upper sublittoral zone

This zone is little known on the south coast of Western Australia. Unfortunately unfavourable conditions in many places prevented its examination by Miss Wollaston. The general aspect—dominance by *Cystophora* species, *Ecklonia radiata*, and *Scytothalia dorycarpa*—appears to be very similar to South Australian coasts, though *C. intermedia* was not observed. Species of *Sargassum* become more prominent on the west coast.

An account by Smith (1952) describes the algal ecology of the Cockburn Sound–Rottnest I. area on the west coast of Western Australia. The reefs in this area show many similarities to the calcareous sand-rock reefs of exposed South Australian coasts, and their algal ecology is also similar. Higher sea temperatures are evident from the slight subtropical element—the greater importance of lithothamnia and of *Sargassum*, and the presence of species such as *Caulerpa racemosa* (Forskål) J. Agardh (f. *cylindracea* (Sonder) Weber van Bosse), *Halimeda cuneata* (=*macroloba* Harvey), and *Penicillus nodulosus* (Lamouroux) Blainville. *Cystophora* is much less important and is largely replaced by species of *Sargassum*. The great similarity in the algal flora, however, is shown in that of some 196 species listed by Smith, about 155 are also found in South Australia.

It is clear that although the south and south-west coasts of Western Australia show many similarities with those in South Australia, distinct changes appear passing west from Esperance. These changes involve the fauna to a greater extent than the flora. Particularly noteworthy are the presence of *Tectarius* in the supralittoral, the absence of barnacles in the mid and upper littoral, and the absence of *Brachyodontes rostratus* and the replacement of several prominent gastropods in the mid littoral. The disappearance of *Hormosira* west of Albany and the gradual decrease in dominance of *Cystophora* spp. up the west coast are the most noteworthy floristic features.

(*d*) *Floristic Comparisons along Southern Australia*

An analysis* of the marine algal flora of southern Australia shows that of some 1010 species of green, brown, and red algae considered, 8 per cent. are cosmopolitan, 32 per cent. range along southern Australia (including Tasmania), 42 per cent. are of eastern affinity (South Australia eastwards), and 16 per cent. are of western affinity, not reaching Victoria. A very few species are known only from the central parts of the southern Australian coast. The eastern group (42 per cent.) may be subdivided into those extending through most of South Australia (about 25 per cent.) and those confined to Victoria and Tasmania (about 17 per cent.).

*Full data to be published elsewhere by H. B. S. Womersley.

A preliminary analysis of the Kangaroo I. algal flora shows that of 482 named species 78 per cent. occur on Victorian coasts, 54 per cent. in Tasmania, and 56 per cent. in Western Australia. Only 22 per cent. of the Kangaroo I. algae occur in New South Wales (compared with 24 per cent. in New Zealand).

Two genera which have been studied recently show similar distributions. In *Sargassum*, subgenus *Phyllotrichia* (Womersley 1954*b*), all five southern species range along southern Australia and Tasmania. Of 14 southern Australian species of *Codium* (Silva and Womersley 1956), 11 range through South Australia and Victoria, 7 of these extending also to Tasmania. Four species occur all along southern Australia and in Tasmania, and 7 along southern Australia but not in Tasmania.

These data indicate that a large proportion of algal species range along southern Australia, with a very considerable eastern element and smaller western element. Of the eastern element, a high proportion is common to South Australia, Victoria, and Tasmania, while a smaller proportion is limited to Victoria or Tasmania, or both.

VI. Discussion and Conclusions

Endean, Kenny and Stephenson (1956) have shown the distinct change from the north Queensland tropical Solanderian Province to the south Queensland and New South Wales warm temperate Peronian Province at about lat. 25° S. Bennett and Pope (1953) have given convincing evidence of a distinct change from the Peronian to a cool temperate province on the extreme east coast of Victoria. They have also shown the similarities of the Victorian and Tasmanian intertidal zonation and organisms. The Victorian and Tasmanian coasts they class as a cool temperate Maugean Province. They further compare this province with the Flindersian to the west, including the South Australian and southern Western Australian coasts. The latter comparisons were made when little information was available about South Australian coasts. In the light of evidence now at hand some of Bennett and Pope's conclusions need modification.

In describing the marine provinces of the Australian coastline it is desirable that they should be of much the same importance, i.e. the differences between them should be of similar magnitude. Endean, Kenny, and Stephenson (1956, Fig. 13) have shown clearly the great changes on the Queensland coast between lats. 25° and 26° S. Here the percentage of southern species changes from nearly 60 per cent. to 20 per cent. and of northern species from just over 10 per cent. to nearly 60 per cent. This, with major changes in the dominant intertidal organisms, shows that the tropical Solanderian and warm temperature Peronian differ markedly.

The differences between the Peronian and Victorian shores are clearly of similar magnitude. It will be evident from the present account, however, that the differences between the Victorian (and Tasmanian) coasts—the Maugean Province of Bennett and Pope—and the South Australian coast (Flindersian as restricted by Bennett and Pope) are of much smaller magnitude. The evidence for this will be further discussed below.

Certain organisms have come to be regarded, often from a world viewpoint, as "warm temperate" and others as "cool temperate". While it may be comparatively

easy to separate tropical, temperate, and arctic or antarctic species, the separation of warm and cool temperate species is not always easy. The kelps—Laminariales—are regarded (e.g. Stephenson 1947, p. 227) as indicators of the cool temperate regions, and are largely absent in warm temperate regions. In the Antarctic Ocean, extending to New Zealand, southernmost Australia, and South America, *Macrocystis* is the most prominent kelp, and in addition a "kelp-like" alga, the giant Fucales genus *Durvillea* (including *Sarcophycus*) has become dominant in the upper sublittoral or lower littoral regions.* *Macrocystis* and *Durvillea* were accepted by Bennett and Pope as indicators of cool temperate conditions, and this is fully justified.

The position along southern Australia is complicated by the high degree of endemism in the algal flora. Many genera, large and small, or groups of species have evolved here and are found nowhere else. The Fucales are a noteworthy case, with genera such as *Cystophora* (about 25 species), *Hormosira*, subgenus *Arthrophycus* of *Sargassum*, and several other small genera. Species of *Cystophora* reach 6 ft in length. It is difficult to say whether such genera should be classed as warm or cool temperate, but with *Durvillea* accepted as a cool temperate alga caution is needed in excluding other Fucales from "cool temperate" when their range coincides in part with that of *Durvillea*. *Phyllospora comosa* is characteristic of the New South Wales coast and (though less prominent) of the Victorian and Tasmanian coasts, but not of the central–west coasts of South Australia. In this case, factors other than temperature must control its distribution.

Of the three Australian kelps (Laminariales), *Macrocystis* is limited to the Tasmanian, Victorian, and eastern South Australian coasts (with a different species in southern and eastern Tasmania from that on the mainland). *Ecklonia radiata* is widely distributed along southern Australia and Tasmania but is more prominent on the New South Wales coast. It is not, however, "a dominant infra-littoral alga . . . in the Flindersian province" (Bennett and Pope 1953, p. 146), but at least on exposed coasts is of minor importance as in Victoria. *Lessonia corrugata* is limited to Tasmanian coasts.

It is now clear that the South Australian, Victorian, and Tasmanian coasts show many similarities; they differ mainly in the presence of *Durvillea* and *Macrocystis* in the slightly colder waters of eastern South Australia, Victoria, and Tasmania. Other cooler-water algae appear in the east, especially in Tasmania, where the mussel *Mytilus planulatus* also becomes more important in sheltered habitats. Our contention is that the coastline of the three States should be grouped as a single province, with the coast east of Robe in South Australia classed as a subprovince. Bennett and Pope (1953, p. 152–3) suggest that Victorian and Tasmanian coasts are very similar, and Guiler (1954, p. 110) supports this. These authors consider that this extended "Maugean" province (first applied to the south and east coasts of Tasmania) is a cool temperate region.

We would suggest then: (i) that the Flindersian Province, which was originally based on the fauna in the vicinity of Adelaide (Hedley 1904; Cotton 1930), extends throughout South Australia, Victoria, and Tasmania; (ii) that eastern South

*In Australia, *Durvillea potatorum* is essentially a sublittoral alga, but in New Zealand (and other subantarctic countries) *D. antarctica* (and *D. willana*) are lower littoral species.

Australia, Victoria, and Tasmania comprise the Maugean subprovince within the Flindersian. The Flindersian Province is of cool temperate affinities, distinctly so in southern Tasmania, grading to an area on the central and west coasts of South Australia which is perhaps best considered as having affinities intermediate between cold temperate and warm temperate regions.

The Flindersian Province has usually been considered to extend around south-west Western Australia as far as Geraldton, intergrading with the tropical Dampierian Province on the west coast (cf. Bennett and Pope 1953, Fig. 5).

Ashby (1924) on the basis of chiton distribution modified the provinces first described by Hedley (1904) by suppressing the Solanderian within the Dampierian, extending the Peronian northwards to Great Sandy I., and introducing an "Indo-Australian region extending from the Abrolhos Islands around south-west Australia into the Great Australian Bight". This overlapped with the Adelaidean (=Flindersian), which extended from Bass Strait as far as Cape Naturaliste. These last two regions represented in Ashby's view two distinct currents, the warm Indian Ocean surface current and the cold western current below, both flowing eastwards along southern Australia (Halligan 1921).

The Indo-Australian region includes the coast where a grading from the typical Adelaidean (Flindersian) to the tropical Dampierian occurs, including the Baudinian region of Kott (1952). The surface warm current and deeper cold current along southern Australia (Halligan 1921) are not stressed by later authors, but the slight spread of warmer-water species around south-west Western Australia may be associated with this warm surface current. Similarly, the reported deeper cold water current passing northward up the Western Australian coast may be the cause of the extension of many typical Flindersian species as far north as the Abrolhos (Hedley 1904; Verco 1912).

Kott (1952) proposed a new zoogeographical province, the Baudinian, to describe the ascidian fauna of the south-west corner of Western Australia (from Perth to Albany). It is very doubtful if the algal distribution would support the recognition of a distinct province here, comparable in status with the other recognized provinces of the Australian coast.

Passing west from South Australia, differences are evident at Esperance in Western Australia (and probably from the first rocky coast some distance east of Israelite Bay). Here *Tectarius rugosus* appears in the supralittoral, barnacles are absent from the mid and upper littoral zones, and *Brachyodontes rostratus* is apparently absent from the mid littoral. Other species disappear gradually around the south-west corner of Western Australia. *Hormosira* is not found west of Albany, *Galeolaria* disappears somewhere north of Cape Naturaliste, and some molluscs are gradually replaced. Near Rottnest I. a tropical influence is appearing, shown by the presence of the algae *Halimeda* and *Penicillus*, and zoanthids, corals, and alcyonarians. The genus *Cystophora* is much less important at Rottnest I. but *C. uvifera* extends as far north as the Abrolhos Is.

Bennett and Pope (1953, pp. 144–6) consider that the New South Wales warm temperate Peronian and their restricted Flindersian (South Australia and south coast of Western Australia) show many similarities. On South Australian coasts,

however, the differences are greater than the similarities. Bennett and Pope (1953, p.144) list six characteristic warm temperate (Peronian) echinoderms, of which two (*Heliocidaris erythrogramma* and *Patiriella gunnii*) are found in South Australia. The first of these is widespread in temperate Australian waters, being an upper sublittoral species in South Australia. Their "typical" Peronian barnacles *Tetraclita rosea* and *Balanus imperator* are not found in South Australia, *Pyura stolonifera* is absent on rocky coasts, and the molluscs show considerable differences. *Tectarius rugosus* and *Clavarizona hirtosa* are not found on South Australian coasts, but appear on the south coast of Western Australia.

The algal differences between New South Wales and South Australian coasts are very considerable, partly because New South Wales is largely outside the southern Australian region of strong algal endemism. The few prominent species in common are widely ranging forms (e.g. *Ecklonia radiata*, *Hormosira banksii*) or ones such as *Phyllospora comosa*, the distribution of which is governed by factors other than temperature. A preliminary analysis of the Kangaroo I. algal flora showed that ony 22 per cent. of the 483 species considered occurred in New South Wales, compared with 78 per cent. in Victoria, 54 per cent. in Tasmania, and 24 per cent. in New Zealand. Any "resemblance between the algal floras of New South Wales and the southern coast of the continent in South Australia" (Bennett and Pope 1953, p. 140, based on Newton and Cribb 1951) does not stand up to detailed analysis.

Sea temperatures support the recognition of one biogeographical province along southern Australia, including Victoria and Tasmania. Figures 2(*a*) and 2(*b*) show mean sea temperatures around Australia during February and August. The whole southern coast of Australia is subject to similar temperatures, 17–20°C in February (summer) and 12–15°C in winter. The waters around Victoria are only about 2°C lower than those in the Great Australian Bight, and those in Tasmania 1–2°C lower again. Such a difference is not usually sufficient to cause a marked change in the flora and fauna (a 5°C difference is usually associated with major changes). Bennett and Pope seem to have unduly emphasized the temperature difference between the waters in Bass Strait and off Kangaroo I. This difference does, however, fit in well with the observed "subprovincial" changes in the intertidal fauna and flora.

Passing from southern Australia up the west and east coast, marked increases of temperature occur. In summer, sea temperatures north of Cape Naturaliste and off the Victorian–New South Wales border are higher than sea temperatures on open coast along southern Australia (except within Spencer and St. Vincent Gulfs). In winter, the sea from about Albany around the south-west corner of Western Australia and from about a quarter of the way up the New South Wales coast is subject to higher temperatures than southern Australian waters.

In conclusion, then, the distribution of algae and animals, the intertidal ecology, and the sea temperatures support the recognition of one geographical province, the Flindersian, along southern Australia. This province grades from the Dampierian of north-west Australia around the south-west corner of Western Australia and includes South Australia, Victoria, and Tasmania. The coast from Robe in South Australia around Victoria and Tasmania forms a subprovince, the Maugean, within the Flindersian. This changes to the warm temperate Peronian on the easternmost

shores of Victoria and in New South Wales, while in the west a gradual transition commences on the rocky coast near Esperance. The large stretches of sandy beach between Eucla and Israelite Bay may provide sufficient barrier between South Australian and Western Australian rocky coasts to account for this change, which would not be expected on sea temperature alone.

VII. Acknowledgments

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EXPLANATION OF PLATES 1–12

PLATE 1

Fig. 1.—Point Sinclair at very low tide. The smooth granite point in the background shows clear-cut zonation; the dark upper band is *Calothrix* in the supralittoral, the light grey bands are *Chamaesipho* and *Catophragmus* in the upper and mid littoral, and the dark band just above water level is the *Balanus*–coralline mat zone of the lower littoral. The calcareous sand-rock reef in the foreground is typical of those on Recent exposed coast.

Fig. 2.—Point Sinclair. Typical zonation on granite. The black *Calothrix* of the supralittoral shows several "*Melaraphe* patches"; below this two barnacle zones (upper and mid littoral) are shown, and part of the lower littoral zone is just exposed.

PLATE 2

Fig. 1.—Point Sinclair. The edge of *Calothrix* in the supralittoral. The sharply defined but irregular edge is shown, with numerous *Melaraphe* on the bare rock below.

Fig. 2.—Point Sinclair. A general view of the barnacle associations of the littoral, passing from *Chamaesipho* on the left through a wide area of *Catophragmus* to *Balanus* near the sea.

PLATE 3

Fig. 1.—Cape Du Couedic. *Chamaesipho columna* (honeycomb barnacle) in the upper littoral.

Fig. 2.—Point Sinclair. *Splachnidium rugosum* association in the mid littoral.

PLATE 4

Fig. 1.—Cape Westall. Mid littoral zone with *Splachnidium rugosum* superimposed on the *Catophragmus* association, and *Galeolaria* prominent on the lower left.

Fig. 2.—Point Sinclair. *Brachyodontes rostratus* as a relatively pure community in the mid littoral. A few *Catophragmus* are present.

PLATE 5

Fig. 1.—Point Sinclair. *Balanus nigrescens* as a pure association in the upper part of the lower littoral.

Fig. 2.—Cape Westall. General view of the lower littoral mat of coralline and other algae covering *Balanus*.

PLATE 6

Fig. 1.—Point Sinclair. The sublittoral fringe of *Cystophora intermedia*. A few *Balanus* are seen on the left.

Fig. 2.—Sleaford Bay. Sand-rock cliffs at the rear of a rock platform showing a good mid-littoral association of *Brachyodontes rostratus*.

PLATE 7

Fig. 1.—Point Sinclair; sand-rock reefs. Mid littoral zone at the rear of a reef, showing prominent patches of blue-green algae (*Symploca hydnoides*), the gastropods *Cellana tramoserica* and a few *Patelloida alticostata*, and scattered *Galeolaria* tubes near *Hormosira* of the lower littoral.

Fig. 2.—Point Sinclair; sand-rock reefs. *Hormosira banksii* on the reef surface (lower littoral).

PLATE 8

Fig. 1.—Point Sinclair; sand-rock reefs. The reef surface, under water, showing dark-coloured algae and whitish nodules of lithothamnia. Two *Haliotis roei* are present.

Fig. 2.—Pennington Bay, Kangaroo I. The "mixed *Cystophora* complex" on the reef surface. On the lower left is *Cystophora siliquosa*; on the lower right and elsewhere is *C. subfarcinata*; the dark-coloured species is *C. uvifera*; and an odd plant of *Hormosira* is present.

PLATE 9

Fig. 1.—Cape Westall. The mid littoral on the sheltered side of rock, showing the distinct subzone of *Galeolaria* with *Cellana tramoserica* and a few *Melanerita melanotragus* just above and *Hormosira* of the lower littoral below.

Fig. 2.—Port Willunga; Aldinga Reef. The upper sublittoral showing the broad thalli of *Ecklonia radiata* and several species of *Sargassum* and *Cystophora*.

PLATE 10

Fig. 1.—Proper Bay, Port Lincoln. *Brachyodontes erosus* association of the lower littoral.

Fig. 2.—Streaky Bay. A general view of the tidal flats, showing the razor shell *Pinna dolabrata* in the lower littoral.

PLATE 11

Fig. 1.—Elliston. The *Posidonia* association within the bay at very low tide.

Fig. 2.—Robe. The lichen *Lichina confinis* well developed in the supralittoral.

PLATE 12

Fig. 1.—Robe. The mid-littoral mollusc association on sand-rock reefs. Mainly *Siphonaria diemenensis*, a single *Cellana* on the left, and a few *Patelloida alticostata*. Blue-green algae and *Galeolaria* are virtually absent here.

Fig. 2.—Robe. *Macrocystis angustifolia* exposed at very low tide just within the bay.

INTERTIDAL ECOLOGY OF SOUTH AUSTRALIAN COASTS

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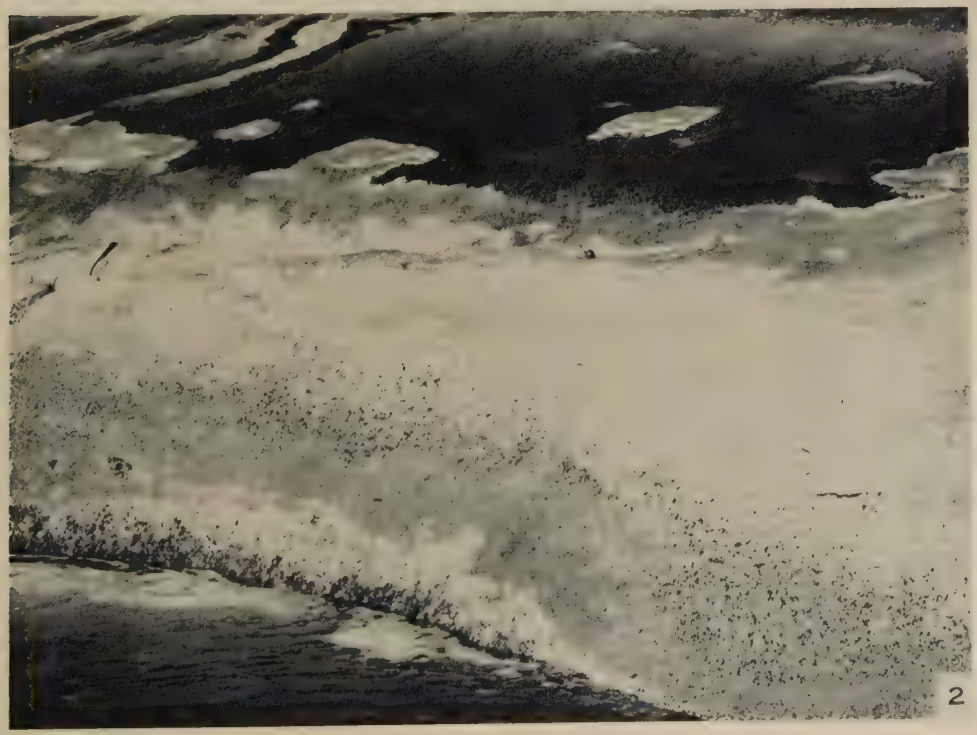

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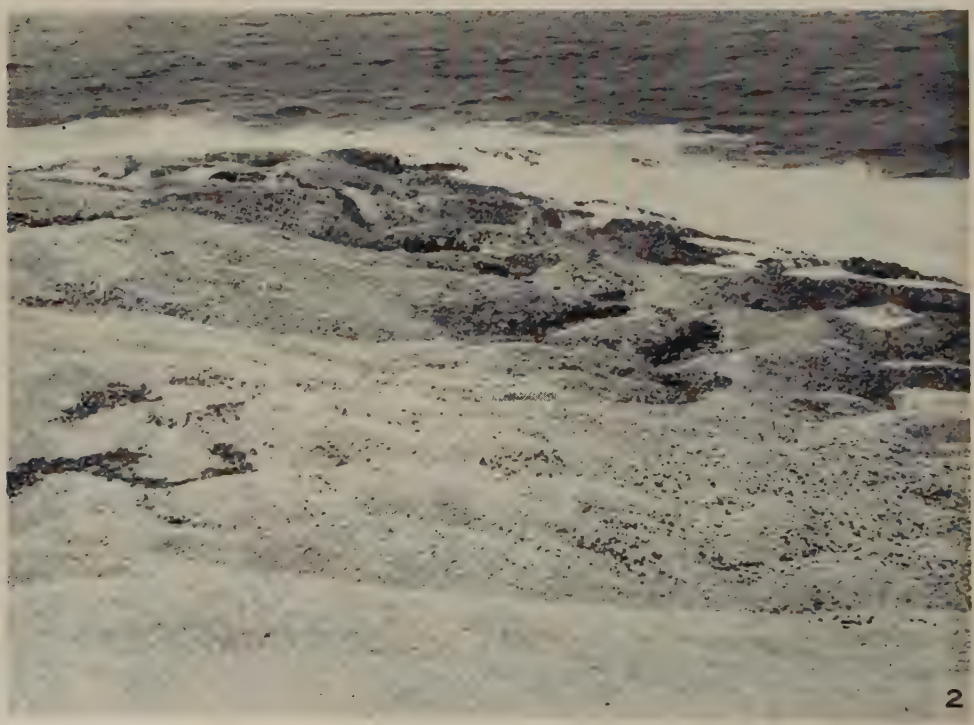

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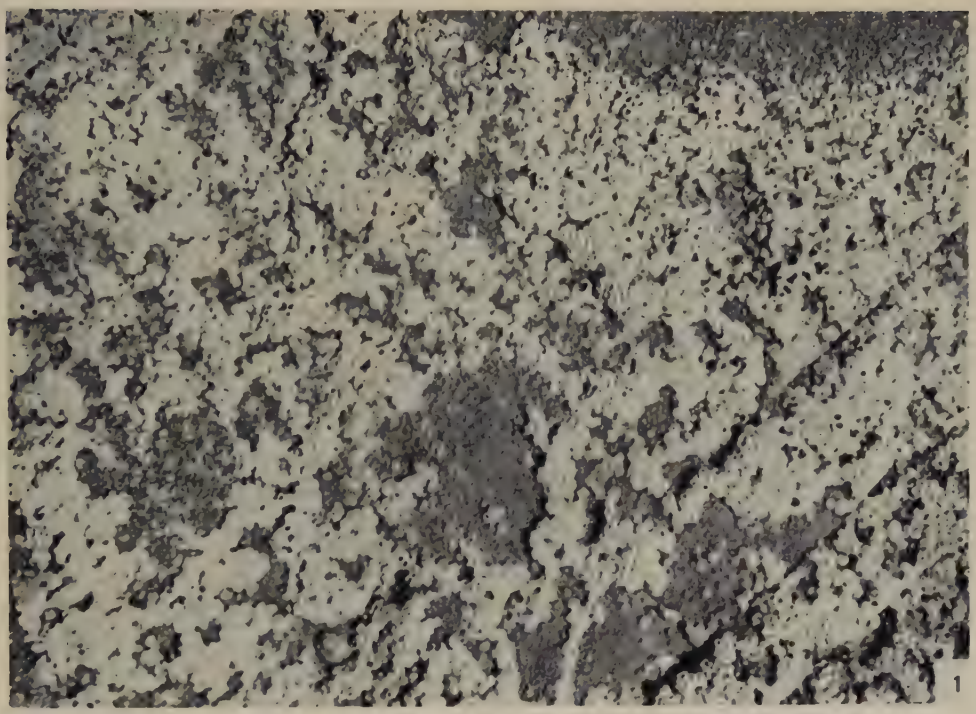

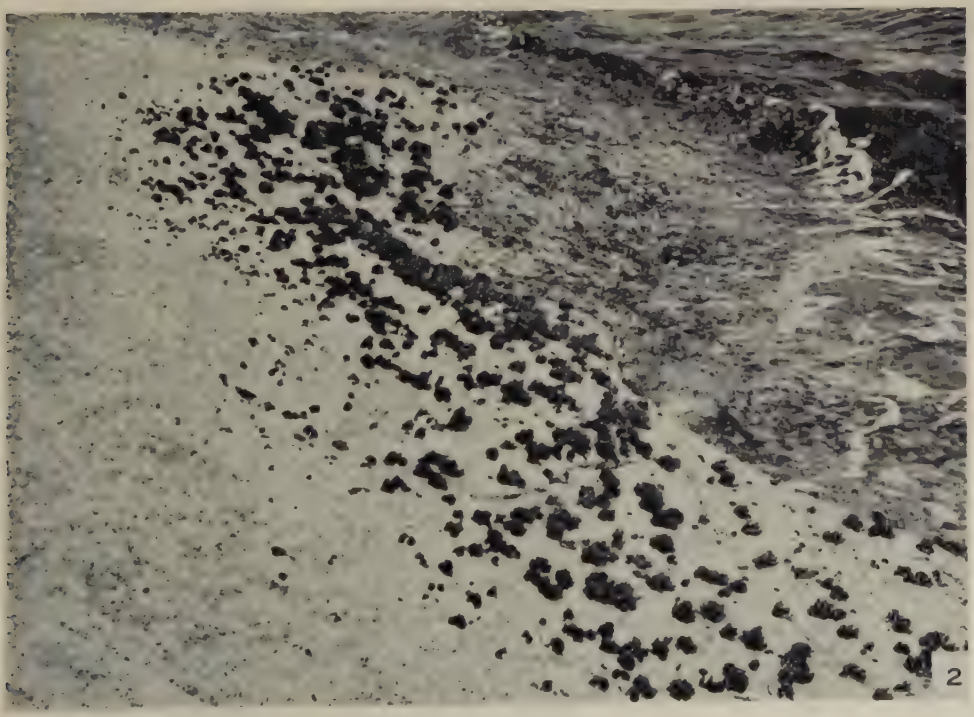

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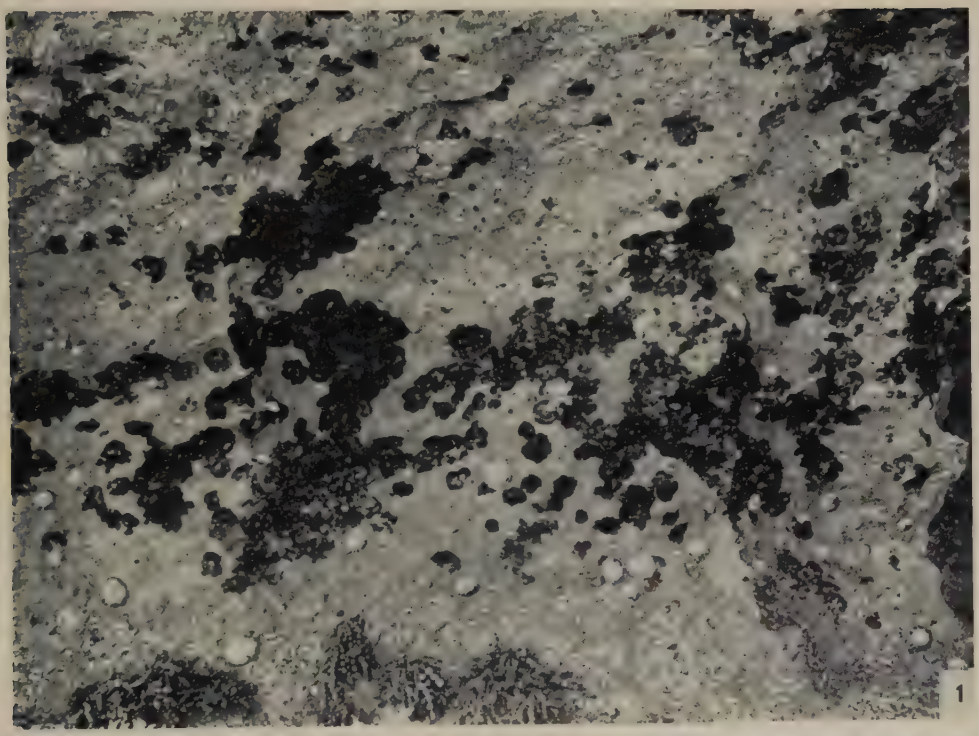

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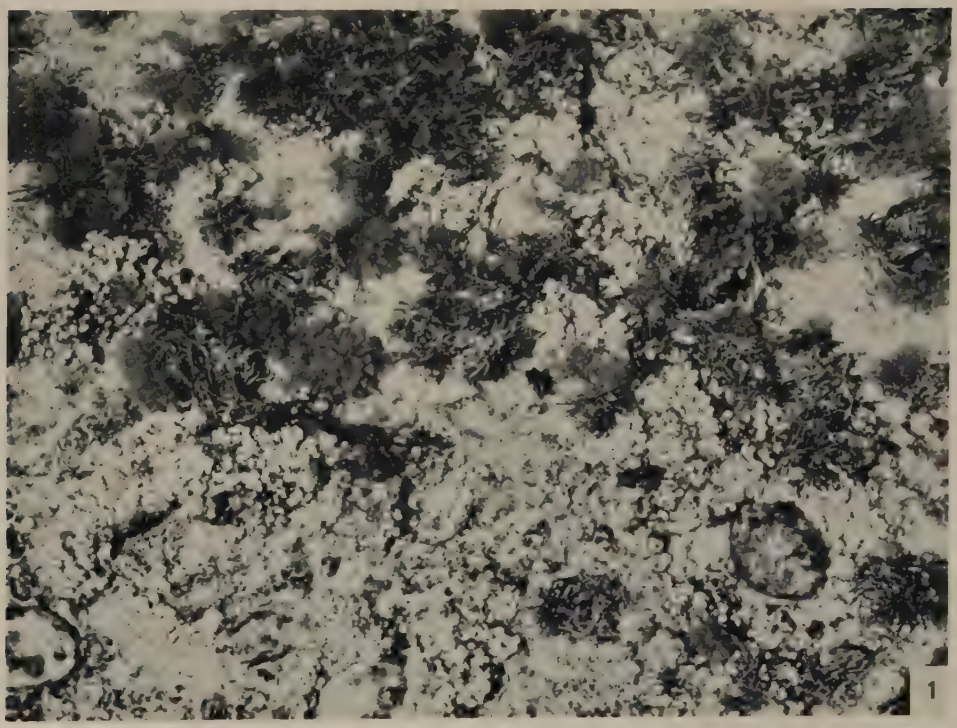

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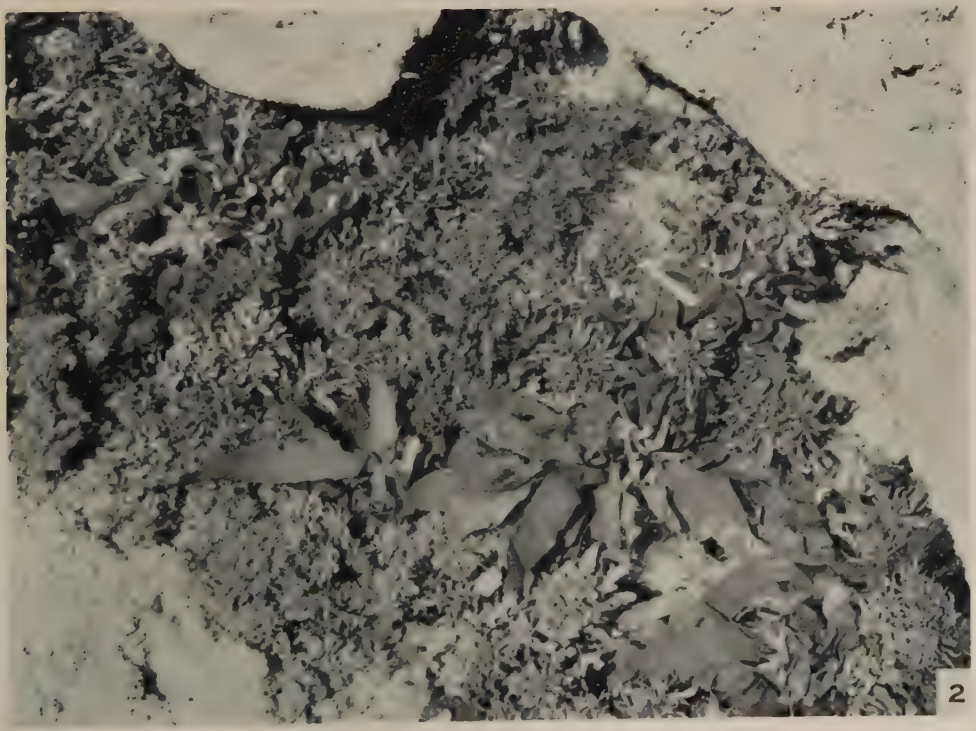

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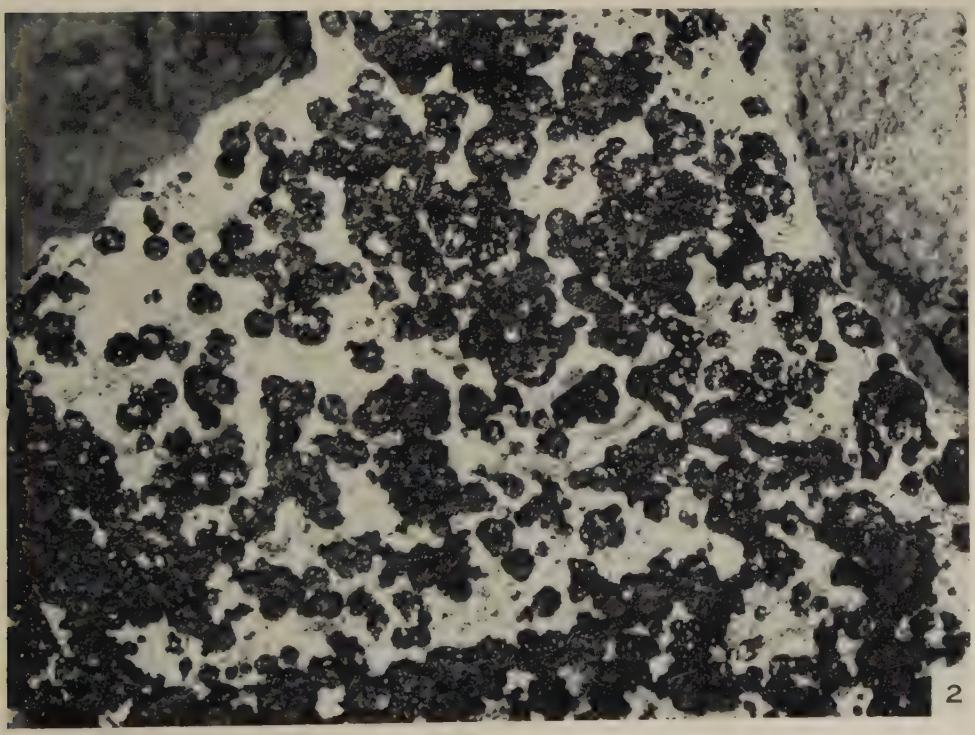

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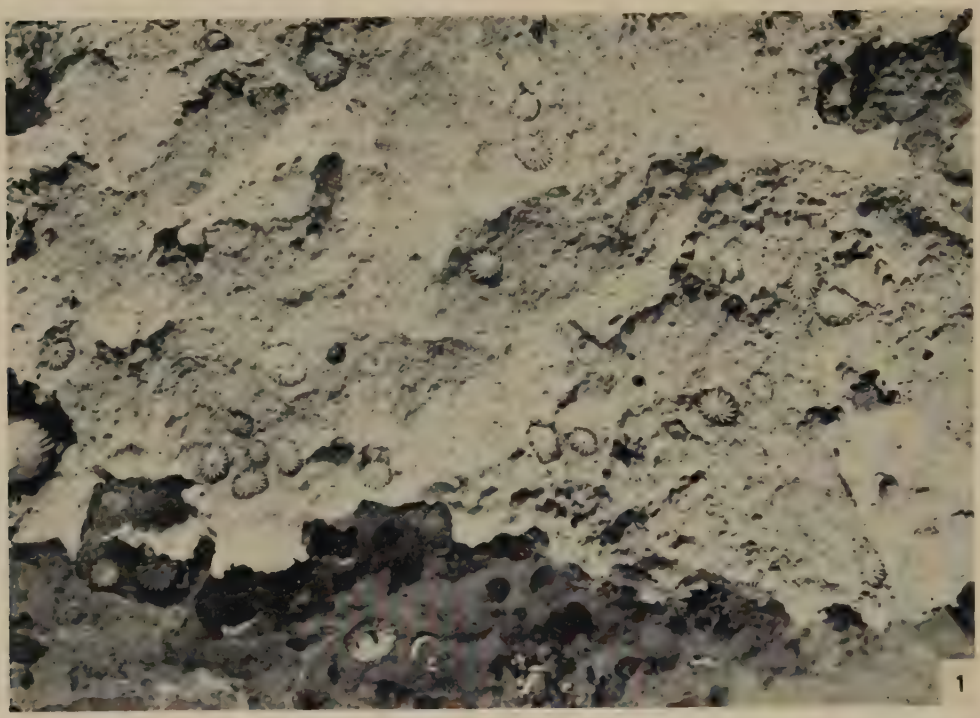

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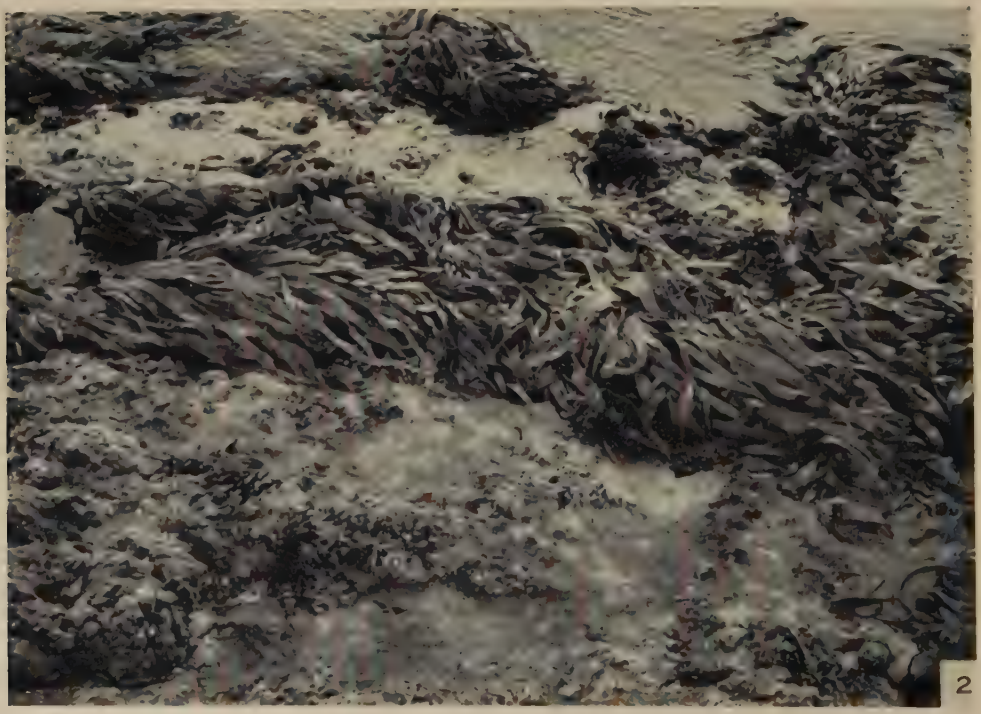

2

AN ECOLOGICAL SURVEY OF THE MARINE FAUNA OF LOW ISLES, QUEENSLAND

By W. Stephenson,* R. Endean,* and Isobel Bennett†

[*Manuscript received October* 23, 1957]

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Summary

The marine fauna of Low Isles was surveyed by the Great Barrier Reef Expedition of 1928–9. A cyclone in 1950 caused damage to the island's coral, and an expedition visited Low Isles in 1954 with the prime objectives of assessing the extent of this damage, and of ascertaining the extent and nature of changes undergone by the island and its fauna and flora since 1929.

It was found that the cyclone had caused great destruction to branching corals but that massive corals had, in most cases, survived. A heavy swell accompanying the cyclone had struck what is normally the lee side of the island, where a dense growth of fragile corals occurred. It is believed that the mechanical force exerted by breaking waves was the chief factor causing the destruction of corals. Coral rubble resulting from this destruction was being rolled about by waves on the seaward slopes of the island, and was hampering recolonization by hard corals. Soft corals, which appeared to have been unaffected by the cyclone, had spread, and appeared to be competing with hard corals for the available substratum.

Alterations in the topography of habitats investigated by the 1928–9 expedition were observed. Some of the shingle ramparts had increased in size, and shingle was encroaching on many of the moats. The mangrove area had increased in extent.

No marked changes in the faunistic composition of the fauna generally had occurred since 1929. However, direct comparison of the results of the 1928–9 expedition with those of the present survey proved difficult. In order to provide a basis for future surveys of the fauna, attempts were made to separate a large number of distinctive habitats, and to list the species found within each of these habitats. The relative abundance of each species found in each habitat was noted, and the general ecology and biogeography of the commoner animals investigated.

I. Introduction

Studies of the ecology of marine organisms found at Low Isles were made by members of the Great Barrier Reef Expedition of 1928–9 (Stephenson *et al.* 1931; Manton and Stephenson 1935). Since 1929, several cyclones have passed near the island. A cyclone in 1934 affected mangroves and corals (Moorhouse 1936), and the head lighthouse keeper at Low Isles reported to the Great Barrier Reef Committee that a cyclone in 1950 had caused great destruction of coral at the island.

An expedition under the auspices of the Great Barrier Reef Committee visited Low Isles from August 12 to 26, 1954. The chief objectives of this expedition were, firstly, to assess the extent of damage to the island, and to its fauna and flora, caused by the cyclone in 1950; and, secondly, to ascertain the extent and nature of changes undergone by the island and its fauna and flora since 1929. Several independent investigations were undertaken, the original surveys of the 1928-9 expedition serving as bases. The present paper is concerned primarily with the ecology of marine animals.

It became apparent soon after work was begun that many habitats and faunistic groups discussed by the 1928–9 expedition required reinvestigation, partly because of suspected changes, and partly because the 1928–9 expedition stressed spectacular animals equally with those which dominated, or were sufficiently common to confer a characteristic facies on, a particular habitat.

Present results are compared with those of the 1928–9 expedition:

(1) To note changes in specific composition of the fauna.

(2) To ascertain whether changes have occurred in the local distribution and abundance of species commonly found in 1928–9 and in 1954.

(3) To group the fauna into more precise habitat categories.

(4) To arrange the fauna within each habitat on a basis of relative abundance of each species.

Also, present results are compared with the results of comparable investigations made in other parts of Queensland and other parts of the Indo-Pacific region.

II. General Environment

(a) *Topographical*

Low Isles (lat. 16° 23′ S., long. 145° 34′ E.) is about 7 miles offshore from Port Douglas and the Daintree River (Fig. 1), and about 20 miles shoreward of the outer Barrier Reefs, which are here tolerably continuous.

At high water two main regions are visible, a small sand cay (*c.*3½ acres) dominated by terrestrial vegetation, and a larger mangrove area (*c.*50 acres). At low water these are joined, and the term "island" is here applied to the total formation. The east-west axis of the island (Fig. 2) is just over a mile in length.

The detailed topography of the island has altered only slightly since the earlier surveys of Stephenson *et al.* (1931) and Fairbridge and Teichert (1947, 1948) were made. Prominent features are: sand cay, reef flat, shingle ramparts, boulder tract, anchorage, and the seaward slopes of the island.

(b) *Hydrological and Climatic*

(i) *Wave Action.*—This is usually slight, and there is no oceanic surge owing to the gradual offshore slope and protection afforded by the outer Barrier Reefs. Wave action is greatest on the south-east of the island, and is appreciable both on the eastern and southern sides, while the anchorage on the north is protected except when northerly winds blow.

Waves associated with cyclonic disturbances come mainly from the east, although waves sometimes come from the north and these seem to cause the greatest damage.

(ii) *Rainfall, Floods, and Salinity.*—Rainfall occurs mostly in summer, and very heavy falls have been reported from nearby Port Douglas. Whilst this rainfall may affect the fauna directly, the indirect effects via Daintree River floods may be more drastic.

Salinity values quoted by Fairbridge and Teichert (1947, 1948) indicate that great dilution can occur at Low Isles during moderate floods.

(iii) *Turbidity.*—The water near the northern Queensland mainland is characterized by a high degree of turbidity (Endean, Kenny, and Stephenson 1956). Orr (1933) found that the average transparency over a period of 1 year at a station 3 miles east of Low Isles was about 12 m, but it would be expected that flooding of the nearby Daintree River would cause a marked increase in the turbidity of the water in the vicinity of Low Isles.

(iv) *Tidal Range.*—Stephenson *et al.* (1931) found at Low Isles an extreme spring range of 10·4 ft and a neap range of about 4 ft. Observation by the present

authors suggested an average spring range of approximately 8 ft and a neap range of approximately 4 ft.

(v) *Currents.*—Data of the Royal Netherlands Meteorological Institute (1949) show that from January to June surface currents within the lagoon between the

Fig. 1.—Queensland, showing localities mentioned in the text.

Barrier Reefs and the mainland are roughly north-north-west. There is considerable variation during the other months as follows: July, west-south-west; August, south-south-east; September, south; October, north-north-east; November, north; December, west. These currents are merely general trends and the presence of tidal streams might well obscure their overall effects.

Fig. 2.—Low Isles, after Stephenson *et al.* (1931), showing the main topographical features and the localities where specimens were collected.

Within the periphery of Low Isles there are local variations in current velocity, and during an ebb tide there are conspicuous drainage areas or channels.

(vi) *Temperatures.*—At Port Douglas, 7 miles from Low Isles, the mean annual range of sea temperatures is 23–28°C and of air temperatures 25–27·5°C, while the extreme recorded range of air temperatures is 10–34°C (Endean, Kenny, and Stephenson 1956).

III. Methods

In the 1928–9 survey each major topographical area was dealt with separately: some areas were treated as units, with comments on the inhabitants; in others there was subdivision into habitats within an area. Since each area consists of a mosaic of diverse habitats (although many different areas contain similar habitats) it was thought desirable in the present survey to deal separately with each habitat. However, topographical unity is preserved by listing them under the same main areas as in the previous survey. The chief results are given in topographical order in Sections V–VIII.

Each area or important subdivision thereof was designated a collecting locality (Fig. 2, roman numerals; references in this paper given in roman capitals are to these localities); and within it observations and collections were made in each major habitat division. In most cases, specimens collected were retained for subsequent examination only if there was some doubt as to their identification.

As the time available for examination of each habitat was restricted, no attempts were made to gauge accurately the population densities of the species encountered. The apparent abundance of each species relative to that of the others present in a particular habitat was determined on a subjective basis. Counts of species were made only in critical cases or when the opinions of the authors differed.

Additional notes were made on outstanding habitat features (e.g. topographical and algal), and particular attention was paid to tide level. On the seaward slopes and in the anchorage the following levels* were estimated: H.W.S., M.H.W., H.W.N., M.S.L., L.W.N., M.L.W., L.W.S., and E.L.W.S. Within the ramparts water is retained above the level of L.W.S., and a new term, "moat level", is necessary. This is the average level of low water in the moats (all low tides) and in actual height is about L.W.N. Within the ramparts below this height, minor differences in level produce major differences in atmospheric exposure.

IV. Index of Species

All species mentioned in the text are tabulated below in systematic order (Tables 1 and 2). It should be noted that this list does not purport to be a complete list of the fauna of Low Isles. *In genera where only one species is mentioned, reference to the species in the main text is by generic name only.*

*Abbreviations used for tidal heights in this paper are: mean high water spring (H.W.S.), mean high water (M.H.W), mean high water neap (H.W.N.), mean sea-level (M.S.L.), mean low water neap (L.W.N.), mean low water (M.L.W.), mean low water spring (L.W.S.), and extreme low water spring (E.L.W.S.).

TABLE 1

LIST OF ANIMAL SPECIES MENTIONED IN TEXT

Species marked with * were not recorded from Low Isles

PROTOZOA

FORAMINIFERA

Marginopora complanata (Lamarck)
(= *Orbitolites complanata* (Stephenson *et al.* 1931))

PORIFERA

Tethya sp.
(Numerous other genera collected. Identifications are awaited.)

COELENTERATA

HYDROZOA

Dynamena crisioides Lamouroux
Millepora alcicornis L.*
M. exaesa Forskål
M. tenera Boschma
Myrionema amboinense Pictet

ZOANTHARIA

Palythoa sp.
Zoanthus sp.

ACTINIARIA

Actinodendron plumosum Haddon
Anthopleura sp.
Arachnanthus sp.
Edwardsia spp.
Phymanthus sp.
Stoichactis kenti (Haddon & Shackleton)

ALCYONARIA

Heliopora coerulea (Pallas)
Lobophytum crassum Marenzeller
L. pauciflorum validum Marenzeller
Nephthea mollis (MacFadyen)
Sarcophyton trocheliophorum Marenzeller
Sinularia conferta gracilis MacFadyen
S. flexibilis (Quoy & Gaimard)
S. polydactyla (Ehrenberg)
S. variabilis Tixier-Durivault
Sphaerella conifera (Tixier-Durivault)
S. echinata (Tixier-Durivault)
Tubipora musica L.

MADREPORARIA

Acanthastrea echinata (Dana)
Acropora brueggemanni (Brook)*
A. corymbosa (Lamarck)
A. cuneata (Dana)*
A. cymbicyathus (Brook)
A. digitifera (Dana)*
A. exilis (Brook)
A. formosa (Dana)
A. glochiclados (Brook)
A. haimei (Milne Edwards & Haime)
A. hebes (Dana)
A. humilis (Dana)
A. hyacinthus (Dana)
A. intermedia (Brook)
A. latistella (Brook)
A. microphthalma (Verrill)
A. patula (Brook)
A. pulchra (Brook)
A. quelchi (Brook)
A. rosaria (Dana)
A. squamosa (Brook)
A. surculosa (Dana)
A. variabilis (Klunzinger)
A. sp.
Coscinaraea columna (Dana)
Cyphastrea chalcidicum (Forskål)
C. microphthalma (Lamarck)
C. serailia (Forskål)
Echinopora lamellosa (Esper)
Favia pallida (Dana)
F. speciosa (Dana)
F. valenciennesi (Milne Edwards & Haime)
Favites abdita (Ellis & Solander)
F. aspera (Verrill)
F. complanata (Ehrenberg)
F. halicora (Ehrenberg)
F. virens (Dana)
Fungia actiniformis (Quoy & Gaimard)
F. echinata (Pallas)
F. fungites haimei Verrill
F. horrida Dana
Galaxea clavus (Dana)
G. fascicularis (L.)
Goniastrea pectinata (Ehrenberg)
G. retiformis (Lamarck)
Goniopora minor Crossland
Herpolitha limax (Esper)
Hydnophora microconos (Lamarck)
Leptastrea purpurea (Dana)
L. transversa Klunzinger
Leptoria phrygia (Ellis & Solander)
Lobophyllia corymbosa (Forskål)
L. hemprichi (Ehrenberg)
Merulina ampliata (Ellis & Solander)
Montipora divaricata Brueggemann
M. erythraea Marenzeller
M. foliosa (Pallas)

TABLE 1 (*Continued*)

MADREPORARIA (*continued*)

M. hispida (Dana)
M. informis Bernard
M. solanderi Bernard
M. spumosa (Lamarck)
M. trabeculata Bernard
M. tuberculosa (Lamarck)
M. turgescens Bernard
M. sp. I
M. sp. II
Oxypora lacera (Verrill)
Parahalomitra robusta (Quelch)
Pavona decusssata (Dana)
P. varians Verrill
P. (*Polyastra*) *obtusata* (Quelch)
Platygyra lamellina (Ehrenberg)
Plesiastrea versipora (Lamarck)*
Pocillopora damicornis (L.)
P. eydouxi Milne Edwards & Haime
P. verrucosa (Ellis & Solander)
Polyphyllia talpina (Lamarck)
Porites andrewsi Vaughan
P. lobata Dana
P. lutea Milne Edwards & Haime
Psammocora contigua (Esper)
Seriatopora histrix (Dana)
Stylophora pistillata (Esper)*
Symphyllia nobilis (Dana)
Turbinaria frondens (Dana)

PLATYHELMINTHES

POLYCLADIDA

Cryptophallus walbergi Boek
Euplana gigas (Schmarda)
Planocera sp.

NEMERTEA

Gorgonorhynchus repens Dakin & Fordham
"*Lineus*" sp.
(Various unidentified species also collected)

POLYZOA

Not identified

ANNELIDA

POLYCHAETA

Arenicolidae
"*Arenicola*" sp.
Amphinomidae
Eurythoë complanata (Pallas)
Aphroditidae (spp.)
Chaetopteridae
Mesochaetopteris minuta Potts
Eunicidae
Eunice antennata Savigny
Glyceridae
Glycera sp.
Nereidae (spp.)
Phyllodocidae
Phyllodoce malmgreni Gravier
Syllidae (spp.)
Sabellidae
Salmacina sp.
Spionidae
Scolecolepis indica Fauvel

OLIGOCHAETA

Pontodrilus bermudensis Beddard

SIPUNCULOIDEA

Aspidosiphon cumingi Baird
(A number of other species collected)

ARTHROPODA

CRUSTACEA

CIRRIPEDIA

Chthamalidae
Chthamulus caudatus Pilsbry
C. malayensis Pilsbry
Lepadidae
Ibla cumingi Darwin
Balanidae
Tetraclita coerulescens (Spengler)
T. squamosa (Bruguiere)
T. vitiata Darwin

ISOPODA

"*Ligia*" sp.
Sphaeromidae (spp.)

AMPHIPODA

Talitridae (spp.)

DECAPODA

Penaeidae
Penaeus sp.

NATANTIA

Hippolytidae
Saron marmoratus (Oliver)
Alpheidae
Alpheus edwardsi (Audouin)

TABLE 1 (*Continued*)

ANOMURA

Hippidae
Emerita analoga (Stimpson)*
Hippa adactyla (Fabricius)

Paguridae
Calcinus gaimardi (H. M. Edwards)
C. laevimanus (Randall)
C. latens (Randall)
Clibanarius padavensis de Man
C. virescens Krauss
Diogenes sp.
Eupagurus janitor Alcock
Pagurus deformis H. M. Edwards
P. fabimanus Dana
P. megistos (Herbst)
Petrolisthes lamarcki (Leach)
Porcellana sp.

BRACHYURA

Dromiidae
Petalomera lateralis (Gray)

Calappidae
Calappa hepaticus (L.)
C. sp.

Grapsidae
Grapsus strigosus (Herbst)
Metapograpsus messor (Forskål)
Sesarma bidens (de Haan)
S. (*Holometopus*) *villosa* (A. M. Edwards)

Hymenosomatidae
Elamena truncata (Stimpson)

Mictyridae
Mictyris longicarpus (Latreille)

Ocypodidae
Macrophthalmus quadratus A. M. Edwards
M. telescopicus (Owen)
Ocypode ceratophthalma (Pallas)
O. cordimana Desmarest
O. kuhli de Haan
Uca dussumieri H. M. Edwards

Portunidae
Portunus granulatus (H. M. Edwards)
P. pelagicus (L.)*
Scylla serrata Forskål
Thalamita admete (Herbst)
T. crenata (Latreille)
T. coeruleipes Jacquinot & Lucas
T. prymna (Herbst)
T. stimpsoni A. M. Edwards

Xanthidae
Actaea hirsutissima (Ruppell)
A. tomentosa (H. M. Edwards)
Atergatis floridus (L.)
Chlorodopsis melanocheirus (H. M. Edwards)
Etisus electra (Herbst)
E. laevimanus Randall
Euxanthus sculptilis Dana
Leptodius exaratus (H. M. Edwards)
Lydia annulipes (H. M. Edwards)
Medaeus granulosus Haswell
Ozius rugulosus Stimpson
Phymodius ungulatus (H. M. Edwards).
Pilumnus vespertilio (Fabricius)

STOMATOPODA

Gonodactylus chiragra (Fabricius)

INSECTA

COLLEMBOLA (1 sp.)

HYMENOPTERA

Oecophylla virescens Fabricius

MOLLUSCA

AMPHINEURA

Acanthozostera gemmata (Blainville)
Schizochiton polyops Iredale & Hull

GASTROPODA

Fissurellidae
Emarginula variegata Adams

Haliotidae
Haliotis asinina L.

Trochidae
Euchelus atratus (Gmelin)
Monodonta labio (L.)
Trochus obeliscus Gmelin
T. niloticus L.

Turbinidae
Turbo nivosus Reeve
T. porphyrites (Martyn)

Neritidae
Nerita albicilla L.
N. annulata Reeve
(= *N. chameleon* (Stephenson *et al.* 1931))
N. lineata Gmelin
N. planospira Anton
N. plicata L.
N. polita L.

TABLE 1 (*Continued*)

Patelloididae
Patelloida saccharina (L.)

Littorinidae
Bembicium melanostoma (Gmelin)
Melaraphe coccinea (Martyn)
M. melanacme (Smith)
M. scabra (L.)
M. undulata (Gray)
Nodilittorina pyramidalis (Quoy & Gaimard)
(= *Tectarius malacannus* (Stephenson *et al.* (1931))
Peasiella tantilla (Gould)

Planaxidae
Planaxis sulcatus (Born)

Telescopiidae
Pyrazus australis (Quoy & Gaimard)*
P. ebeninus Bruguiere*
Telescopium telescopium (L.)
Terebralia palustris (L.)
(= *Pyrazus palustris* (Stephenson *et al.* 1931))

Cerithiidae
Cerithium dorsuosum Mencke
C. jannelli Hombron & Jacquinot
Rhinoclavis vertagus (L.)

Vermetidae (spp.)

Strombiidae
Lambis lambis (L.)
Strombus gibberulus L.
S. luhuanus L.
S. variabilis Swainston

Pyramidellidae
Pyramidella maculosa Lamarck

Heliocidae
Toronista variegata (Gmelin)

Cypraeidae
Amphiperas ovum (L.)
Arabica arabica (L.)
Cypraea tigris L.
Monetaria annulus (L.)
M. moneta (L.)*

Naticidae
Mamilla sebae (Souleyet)
Natica violacea Bruguiere
Notocochlis gualteriana (Recluz)
Uber conicum (Lamarck)*
U. pyriformis (Recluz)
U. strangei (Reeve)*

Muricidae
Gyrineum pulchellum (Forbes)
Mancinella pica (Blainville)
Morula anaxares Kiener
M. concatenata (Blainville)
M. margariticola (Broderip)
M. marginalba (Blainville)

Pyrenidae
Engina melanozona Tomlin

Nassariidae
Nassarius coronatus (Bruguiere)
N. lurida (Gould)
Neotha albescens (Dunker)
Phos rufocinctus Adams

Buccinidae
Cantharus fumatus Reeve
Pollia balteata (Reeve)

Volutidae
Cymbiola pulchra (Sowerby)
Melo amphorus (Solander)

Olividae
Oliva caerulea (Bolten)
O. erythrostoma (Meuschen)

Conidae
Conus capitaneus L.
C. marmoreus L.
Darioconus textile (L.)

Turridae (spp.)

Terebriidae
Terebra affinis Gray
T. muscaria Lamarck

Aplysiidae
Aplysia angasi (Sowerby)
Dolabella scapula (Martyn)

Siphonariidae
Siphonaria marza (Iredale)
S. zanda (Iredale)
(= *S. denticulata* (Stephenson *et al.* 1931))

Ellobiidae
Cassidula spp.
Quoyia decollata (Quoy & Gaimard)

Onchidiidae
Onchidium buetschli Stantshinsky
O. verruculatum Cuvier

PELECYPODA

Solemyidae
Solemyarina terrereginae Iredale

TABLE 1 (*Continued*)

Arcidae
Navicula ventricosa Lamarck
Ustularca cruciata (Phillippi) *venuta* Iredale
(= *Arca fusca* (Stephenson *et al.* 1931))
Isognomontidae
Isognomon isognomon L.
Perna nucleus Lamarck
(= *Melina nucleus* (Stephenson *et al.* 1931))
Pteriidae
Pinctada margaritifera (L.)
Pinnidae
Atrina gouldi (Reeve) *banksiana* Iredale
(= *Pinna vexillum* (Stephenson *et al.* 1931))
Ostraeidae
Crassostrea amasa (Iredale)
(= *Ostrea mordax* (Stephenson *et al.* 1931))
C. echinata (Quoy & Gaimard)
C. commercialis (Iredale & Roughley)*
Spondylidae
Spondylus ducalis Bolten
Limidae
Promantellum parafragile Iredale
(= *Lima tenera* (Stephenson *et al.* 1931))
Anomiidae
Anomia sp.
Mytilidae
Brachyodontes rostratus (Dunker)*
Lithophaga dichroa Iredale
Modiolus agripeta Iredale
Modiolus spp.
Trichomya hirsuta (Lamarck)*
Carditidae
Cardita variegata Bruguiere
Chamidae
Chama jukesi Reeve
Lucinidae
Codakia simplex Reeve
Loripes haddoni Melville & Standen
Cardiidae
Cardium oxygonum (Sowerby)
Regozara flava (L.)
Tridacnidae
Tridacna crocea Lamarck
T. derasa (Bolten)
T. fossor Hedley
Hippopus hippopus (L.)
Veneridae
Chione costellifera (Adams)
Circe pectinata (L.)
C. tumidum (Bolten)
Lioconcha fastigata (Sowerby)
Periglypta puerpera (L.)
Tellinidae
Arcopagia remies (L.)
(= *Tellina remies* (Stephenson *et al.* 1931))
Tellina crucigera Lamarck
Gariidae
Asaphis deflorata (L.)
Amphidesmatidae
Atactodea striata (Gmelin)
Davila plana (Hanley)
Geloinidae
Geloina coaxans (Gmelin)
(= *Cyrena coaxans* (Stephenson *et al.* 1931))

ECHINODERMATA

ASTEROIDEA

Archasteridae
Archaster typicus Müller & Troschel
Oreasteridae
Culcita novaeguineae Müller & Troschel
Protoreaster nodosus (L.)
Asteropidae
Asterope carinifera (Lamarck)
Ophidiasteridae
Fromia milleporella (Lamarck)
Linckia laevigata (L.)
Nardoa novaecaledoniae (Perrier)
N. pauciforis (von Martens)
Asterinidae
Patiriella exigua (Lamarck)
Echinasteridae
Echinaster luzonicus (Gray)

OPHIUROIDEA

Ophiomyxidae
Ophiomyxa australis Lutken
Amphiuridae
Ophiactis savignyi (Müller & Troschel)
Ophiotrichidae
Macrophiothrix longipeda (Lamarck)
Ophiocomidae
Ophiarthrum elegans Peters
O. pictum (Müller & Troschel)
Ophiocoma erinaceus (Müller & Troschel)
O. scolopendrina (Lamarck)
Ophiomastix asperula Lutken
Ophiodermatidae
Ophiarachna incrassata (Lamarck)
Ophiarachnella gorgonia (Müller & Troschel)
O. septemspinosa (Müller & Troschel)
Ophiolepididae
Ophiolepis superba Clark

TABLE 1 (*Continued*)

ECHINOIDEA

Centrechinidae
Diadema setosum (Leske)

Echinidae
Tripneustes gratilla (L.)

Echinometridae
Echinometra mathaei (Blainville)

Laganidae
Laganum depressum Agassiz

Echinoneidae
Echinoneus cyclostomus Leske

HOLOTHURIOIDEA

Cucumariidae
Discucumaria africana (Semper)

Stichopodidae
Stichopus chloronotus Brandt
S. horrens Selenka
S. variegatus Semper

Holothuriidae
Holothuria arenicola Semper
H. argus (Jaeger)
H. atra Jaeger
H. coluber Semper
H. impatiens (Forskål)
H. leucospilota (Brandt)
H. martensi Semper
H. pardalis Selenka
H. scabra Jaeger
Actinopyga miliaris (Quoy & Gaimard)

Synaptidae
Polyplectana kefersteini (Selenka)
Synapta maculata (Chamisso & Eysenhardt)

Chiridotidae
Polycheira rufescens (Brandt)

CHORDATA

TUNICATA

Ascidiacea (spp.)

ENTEROPNEUSTA

Balanoglossus carnosus (Willey)
Ptychodera flava Eschscholtz

ELASMOBRANCHII

Hemiscyllium ocellatum (Bonaterre)

TELEOSTEI

Abudefduf sp.
Epinephelus merra Bloch
Epinephelus sp.
Lutianus argentimaculatus (Forskål)
L. fulviflamma (Forskål)
Parioglossus rainfordi McCulloch
Periophthalmus koelreuteri (Pallas)
Plectorhinchus sordidum (Klunzinger)
Pseudupeneus indicus (Shaw)
Ophichthys cephalozona (Bleeker)
O. vesicolor (Richardson)
Salarias meleagis (Cuvier & Valenciennes)

TABLE 2

LIST OF PLANT SPECIES MENTIONED IN TEXT

Species marked * were not recorded from Low Isles

SPERMATOPHYTA

Avicennia marina L.
Bruguiera gymnorhiza Lamarck
(= *B. rheedi* Stephenson *et al.*)
Ceriops tagel (Perrottet) C. E. Robinson
Halophila ovalis (R. Brown) J. D. Hooker
Rhizophora mucronata Lamarck
Sesuvium portulacastrum L.
Thalassia hemprichii (Ehrenberg) Ascherson
*Zostera**

ALGAE

*Amphiroa**
Dictyosphaeria versluysii Weber van Bosse
Enteromorpha clathrata (Roth) J. Agardh
Gelidium sp.
Halimeda opuntia (L.) Lamouroux
H. mossile (Ellis & Solander) Lamouroux
"Lithothamnion" sp.
Padina sp.
"*Sargassum*" sp.
Turbinaria ornata (Turner) J. Agardh
T. conoides (J. Agardh) Kuetz

V. The Sand Cay

The periphery of the sand cay consists of areas of steeply sloping sand, and areas where beach rock predominates. Both sand and rock are derived from coral. The sizes and positions of the sandy and rocky areas change periodically (Moorhouse 1936; Fairbridge and Teichert 1947).

In August 1954 there was no trace of the eastern sector of beach rock noted by Stephenson *et al.* (1931), but the northern sector was still extensive. The head lighthouse keeper, Mr. Chapman, reported that even this northern area had been

Table 3
FAUNA OF THE BEACH ROCK (LOCALITY XV)

Ecological Significance	H.W.N.	M.S.L.	L.W.N.	Moat Level
Dominant	*Nodilittorina* *Planaxis*	*Crassostrea amasa*	*Enteromorpha*	*Chama*
Subdominant or very common			*Siphonaria zanda* *Onchidium verruculatum* Vermetidae (1 sp.)	*Spondylus* *Onchidium verruculatum* Vermetidae (1 sp.) *Clibanarius virescens*
Common or present	*Melaraphe coccinea* *M. melanacme* *M. undulata* *Nerita plicata* *N. polita*	*Onchidium verruculatum* *Morula marginalba* *Patelloida* *Acanthozostera** *Anthopleura** *Perna*	*Patelloida* *Monodonta* *Cantharus* *Tetraclita vitiata* (seaward face only) *Perna** *Anthopleura**	*Patelloida* *Mancinella* *Tetraclita vitiata* *T. coerulescens* *Anthopleura** *Acanthozostera** *Navicula** *Ustularca**

*Species typically inhabiting crevices.

sand-covered since 1952. Possibly it is only a temporary habitat for rock-living forms, but against this, its population density suggests only an occasional covering, with survival of most of the population.

(*a*) *Steeply Sloping Sand* (XIX(*a*), (*b*))*

The 1928–9 expedition recorded ghost crabs (*Ocypode ceratophthalma* and *O. cordimana*) from this habitat. A distinct *Ocypode* zone occurred in 1954, typically at H.W.S., but moving to about M.H.W. during neap tides. The only specimen collected was *O. kuhli*, previously unrecorded in Queensland.

The middle of the slope was devoid of permanent inhabitants, but at about L.W.N. near the sand flat, *Davila* formed a zone. Unidentified talitrids were very

*Roman capitals relate to the collecting localities shown in Figure 2 (see Section III).

common and isolated mole crabs (*Hippa*) and olive shells (*Oliva caerulea* and *O. erythrostoma*) were also found.

(*b*) *Beach Rock* (XV)

Three habitats were recognizable:

(i) *On Rock Surfaces* (Table 3; Plate 1, Fig. 2).—Four fairly distinct zones were present: "bare", oyster, algal, and *Chama* zones. The "bare" uppermost zone was literally bare through sand abrasion except at its western end, where a brown algal encrustation occurred. Here littorinids dominated the upper half of the zone and *Planaxis* dominated the lower half.

TABLE 4
UNDER-ROCK FAUNA, BEACH ROCK (XV)

Ecological Significance	M.S.L.	Moat Level
Dominant	*Petrolisthes*	*Clibanarius virescens*
Very common	*Onchidium verruculatum* *Gonodactylus* Talitridae (spp.) *Ozius*	*Petrolisthes* *Holothuria impatiens* *Ophiarthrum elegans* Porifera (more than 3 spp.)
Common or present	*Leptodius* *Grapsus* *Sesarma bidens* "*Ligia*" Diplopoda (1 sp.) *Morula anaxares* *Euchelus* *Patiriella* *Polycheira* Sipunculoidea (1 sp.)	*Leptodius, Pilumnus, Lydia, Petalomera, Macrophthalmus quadratus, Elamena, Thalamita stimpsoni, Porcellana, Pagurus deformis, Engina, Gyrineum, Nerita albicilla, Navicula, Ustularca, Spondylus, Anomia, Eunice, Eurythoë,* Syllidae (1 sp.), numerous Porifera and Polyzoa.

(ii) *Within the Rock.*—This habitat was not intensively studied. From about M.S.L. downwards, boring forms were evident. *Lithophaga* was clearly dominant and was accompanied by sipunculids. Otter (1937) gives full lists of species found in this habitat.

(iii) *Under Rocks* (Table 4; Plate 2, Fig. 1).—The seaward-dipping beach rock weathers into large flat slabs. Two collections were made, one at M.S.L. and the other at moat level (northern moat), and the following points are noteworthy: (1) the diversity of the fauna, especially in the collection made at moat level; (2) the dominance of Crustacea. The stones are evidently a refuge for Crustacea, although some, especially "*Ligia*", *Grapsus*, *Sesarma bidens*, and *Clibanarius virescens*, move out during the day at low water. A millipede was found commonly under rocks but was not a temporary terrestrial invader. Specimens in a similar habitat have been obtained at Point Vernon on the mainland coast.

VI. The Reef Flat

Stephenson *et al.* (1931) divided this into the mangrove swamp, mangrove park, moats, rocky area, *Thalamita* flat, and sandy areas.

A channel draining northwards into the anchorage divides the reef flat into a western section virtually without mangroves, and a large eastern section dominated by mangroves, and often muddy. Each forms a graded series of habitats.

In the western section the sand flat grades into the *Thalamita* flat, where the water is deeper and stones are common. As a result of further deepening of water the *Thalamita* flat grades into a series of peripheral moats. The northern moat, which is separated from the western flat by the boulder zone, cay, and anchorage, is ecologically part of the western section. This section appears to have undergone little change since 1928–9 although the *Asterina* spit has increased in size, as Fairbridge and Teichert (1947, 1948) noted, and the moats are smaller.

In the eastern section, the dominant feature is the muddy mangrove swamp. To the east it merges with the shingle ridges, and to the west it thins out (mangrove park) to isolated specimens of *Rhizophora*, which invade a flat, rocky, and sandy area ("honeycomb" rock). To the south and south-east, the swamp is bordered by small peripheral moats, while to the north-west large mangroves just invade the largest unit in the moat system, the *Porites* pond. The moats form the most important ecological link between the two halves of the flat.

Since 1928–9 the eastern section of the reef flat has changed considerably. The north-east moat has disappeared, presumably as a result of the 1934 cyclone (Fairbridge and Teichert 1947, legend to Plate IV). The extent of the south-eastern moat system has been reduced, and in the south-south-east some of the moats, which were well developed in 1928–9, are barely recognizable at present. The *Porites* pond has been, and is being, encroached upon along its western side by shingle from the *Tripneustes* spit, which has increased to such a height as to be continuous with the shingle mound of the key chart of Stephenson *et al.* (1931). Additional shingle has been thrown up on the eastern side of the mangrove area, adding to and further complicating the rampart system. The area dominated by mangroves has increased, and the dense area has extended westwards. Recent *Rhizophora* seedlings are sparsely distributed over an extensive area in the *Porites* pond, the madrepore moat, and even on the sand flat adjacent to the cay. Seedlings of *Avicennia* were also scattered on the rubble foreshore outside the ramparts on the eastern side of the island.

(*a*) *The Mangrove Swamp*

Stephenson *et al.* (1931) considered the mangrove swamp and the mangrove park separately but these have sufficient in common to justify treatment as one unit. Previously, the swamp was divided into five areas (dense woodland, sandy pools, passages into swamps, muddy glades, and shingle tongues) and the outstanding features of the flora and fauna were described. Here it is considered preferable to deal separately with the main habitats, and to consider each in its different manifestations.

Three main habitats are distinguished: (i) on mangroves; (ii) in mangrove wood; (iii) on and within the surrounding substratum. The substratum varies considerably and includes: thick soft mud in the centre of the swamp; dirty shingle on its eastern side merging with clean shingle on the eastern ramparts; sand and grit in the south-east corner of the mangrove area; clean sand in passages into the swamp, particularly on the western side and also in the drainage channel leading to the easterly "new gap" (Fairbridge and Teichert 1947); predominantly rocky areas in the extreme west (mangrove park and honeycomb rock areas).

(i) *On Mangroves.*—On all the taller mangroves (*Rhizophora*, *Avicennia*, *Bruguiera*, *Ceriops*), a *Melaraphe scabra* zone was present. The zone extended, where the habitat permitted, from about 3 ft above H.W.S. to about H.W.N. In sheltered muddy areas *Nerita lineata* occurred as a subdominant form about M.H.W. downwards.

From H.W.N. downwards the fauna varied depending on the locality examined. In clean sandy peripheral areas where the habitat extended almost to moat level, a distinct oyster zone (*Crassostrea amasa*) was present (e.g. XXIX, mangrove park; Plate 2, Fig. 2). Other animals encountered were: *Perna*, *Acanthozostera*, an unidentified anemone, *Siphonaria marza*, *Tetraclita vitiata*, *Nerita annulata*, *Metapograpsus*, and *Clibanarius virescens*. Most of these species also occurred on the beach rock.

In clean sandy areas amongst mangroves, rather than on their periphery, the oyster zone was absent, and at the equivalent levels the trunks and roots were bare (e.g. XXX, sandy glade through mangroves). Possibly settlement of oyster spat was prevented as a result of sand abrasion.

One clean sandy area (XXXVII) which was especially noteworthy because of its coral fauna (see below) was also unusual in that a barnacle zone extended from H.W.N. to L.W.N. *Tetraclita vitiata* was dominant, with *Chthamalus caudatus* common, and *Tetraclita coerulescens* present. *Crassostrea echinata*, *C. amasa*, *Monodonta*, and *Nerita planospira* were also found. This is an unusual mangrove fauna, being more typical of rocks.

Towards the south-east of the mangrove area sand and grit predominated (XXXII; Plate 3, Fig. 1). Here mangroves were only found above M.H.W. *Cerithium jannelli* and *Nerita planospira*, both very common on the substratum, were co-dominant on the lower mangrove stems. *Crassostrea amasa* and *Chthamalus caudatus* were present. and also *Peasiella*, a typical, but never abundant, inhabitant of coastal rocks in Queensland.

In the muddy but fairly open areas near the eastern edge of the swamp (XXXIX) from H.W.N. downwards, gastropods predominated with *Nerita lineata*, *N. planospira*, and *Cerithium janelli* codominant. A few specimens of *Crassostrea amasa* were still present, and several crabs were common in and amongst the lower stems (*Clibanarius padavensis*, *Sesarma* spp., and *Metapograpsus*).

In the muddy enclosed areas near the centre of the swamp, from H.W.N. downwards, the fauna was sparser, with a few specimens of *Nerita lineata* and *Crassostrea echinata* only.

Below moat level, the roots of *Rhizophora* could be considered as part of the general moat environment. However, they carried a characteristic hydroid, *Myrionema*, which did not occur in similar density elsewhere. This species was

most common in the sandy glades, and seemed to require mud-free conditions, a moderate water current, and 9 in. or more of water. On the mangrove roots sponges and ascidians were common. Corals were also present, being most common in the clean eastern drainage channel from the mangroves (XXXVII). Here, in addition to species of the general substratum, the following were attached to *Rhizophora* roots: *Leptastrea purpurea* (very common), *Pocillopora damicornis* (common, colonies to 8 in. diameter), encrusting *Millepora* sp. (colonies up to 10 by 6 in.), *Porites lobata* (few), and *Coscinaraea* (one only).

TABLE 5

FAUNA OF MANGROVE SHINGLE HABITATS

	XXXIV, XXXVIII M.H.W. to H.W.S.	XXXIX(1) H.W.N.	XXXIX(2) L.W.N.
Ecological Significance	Shingle with sandy grit compacted beneath and bearing *Sesuvium*	Coarse brown shingle with muddy sand	Muddy shingle with muddy grit
Surface and immediately subsurface fauna: Dominant	*Quoyia* *Bembicium*	*Quoyia*	*Cerithium jannelli*
Very common	*Nerita annulata* *Planaxis* *Onchidium buetschli* Talitridae (spp.)	*Nerita annulata* *Bembicium* *Cassidula* spp.	*Bembicium* *Nerita annulata* *Cassidula* spp. *Quoyia*
Present or common	*Metapograpsus* *Nerita plicata* "*Ligia*" Arachnida (1 sp.) Diplopoda (1 sp.) *Melaraphe scabra* *M. undulata*	*Onchidium buetschli*	*Clibanarius padavensis* *Circe tumidum* *Leptastrea purpurea* (in drainage channel)
Additional subsurface fauna	*Pontodrilus* *Uca dussumieri* *Sesarma villosa* Other crabs	*Sesarma bidens* *S. villosa*	*Parioglossus* *Sesarma bidens* *S. villosa* *Planocera*

Leptastrea and *Pocillopora* were also attached to *Rhizophora* in sandy localities to the north-west and west of the mangroves (e.g. VIII, XXX) where *Montipora divaricata* was often present, either alive (VIII) or recently dead (XXX). *Leptastrea* extended into muddy areas, where small colonies lived on *Rhizophora* roots in slight drainage trickles (e.g. near XXXVII, at XXXIX). It tolerates extreme environments, and is common in coastal pools in tropical Queensland.

Rhizophora roots (Plate 3, Fig. 2) also formed effective refuge for fish including *Hemiscyllium*, *Epinephelus merra*, an undentified species of *Epinephelus*, *Lutjanus argentimaculatus*, *L. fulviflamma*, *Plectorhinchus*, and *Pseudupeneus*.

(ii) *Within Mangrove Wood.*—The fauna was not sampled intensively, but general observations suggested that with increasing age of the mangroves a sequence of decay was initiated by "shipworms" followed by sphaeromids. Fallen mangroves lay in muddy environments and were inhabited by grapsid crabs (e.g. *Metapograpsus* and *Sesarma*) and fishes (e.g. *Parioglossus* and *Periophthalmus*).

(iii) *Within the Substratum.*—Two of the six substrata within the mangrove area (clear shingle and honeycomb rock) contained species not typically found in association with mangroves and are considered in Section VII. The other four are described below.

(1) *Mud* (XXXIX; Plate 4, Fig. 1).—*Telescopium* was dominant in the shallow pools and *Terebralia* on the emergent mud. On the shells of both, occasional specimens of *Crassostrea amasa* were found. Other common surface forms were

TABLE 6

SURFACE FAUNA OF CLEAN SAND, GRIT, AND SHINGLE NEAR MANGROVE (XXXII)

Ecological Significance	H.W.N. (in Shade)	M.S.L. (outside Shade)
Dominant	*Anthopleura*	*Nerita planospira*
Very common	*Nerita planospira* *Cerithium dorsuosum*	*Nerita polita* *Clibanarius virescens* *Modiolus*
Present or common	*Circe tumidum* *Asaphis*	*Medaeus* *Cerithium dorsuosum* *Onchidium verruculatum* *Pollia*

Periophthalmus and an unidentified species of *Penaeus*. The *Terebralia*-dominated areas bore numerous *Sesarma* burrows, and other species of crabs, which evaded collection, were noted. *Geloina* was evidently present and piles of shells left by pearling crews were still found.

(2) *Shingle with Grit and Sand.*—This occurred to the east of the dense mangrove area. Collections were made in a higher environment of shingle and sandy grit (e.g. XXXVIII; Plate 4, Fig. 2), and a lower one of muddy shingle with muddy grit (XXXIX(2); Plate 5, Fig. 1). The fauna (Table 5) was dominated by molluscs and was poorer in the lower situation. Possibly muddiness eliminated some species. The upper fauna was augmented by some semiterrestrial animals including an isopod, a spider, a millipede, and an earthworm. Throughout the only true "mangrove species" was *Melaraphe scabra*, but local dependence upon mangroves in the upper environment was indicated by a concentration of *Quoyia*, *Bembicium*, and *Onchidium buetschli* under the shade of *Bruguiera*.

(3) *Clean Sand, Grit, and Shingle* (XXXII; Plate 3, Fig. 1).—Collections were made within shade at about H.W.N. and outside the shaded area at about M.T.L. The fauna (Table 6) differed from the previous mangrove–shingle habitats, and none of the species was restricted to mangroves. Most were characteristic of gritty

TABLE 7

FAUNA OF THE SAND FLAT (XIX, XX, XXI, XXIII)

Ecological Significance	Rubble Area			Sandy Area	
	On Surface	Under Non-embedded Stones	Under Embedded Stones	On Surface and Immediately Below	By Digging Only
Dominant	*Marginopora* *Archaster*	*Clibanarius virescens*	*Ptychodera* *Edwardsia*	*Strombus gibberulus* *Marginopora*	*Edwardsia* *Ptychodera*
Very common	*Clibanarius virescens*	*Thalamita admete* *Leptodius*	*Eurythoë*	*Archaster*	"*Arenicola*" *Scolelepis* *Aspidosiphon* Sipunculoidea (2 spp.) *Loripes* *Edwardsia* (2 spp.) *Atactodea*
Present or common	*Strombus gibberulus* *Nassarius lurida* *Phos* *Actinodendron*	*Calcinus latens* *Ophiarthrum elegans* *Morula concatenata* *Eurythoë* Aphroditidae *Cardita* *Etisus electra*	*Nereidae* *Alpheus edwardsi*	*Nassarius lurida*, *Phos*, Turridae, *Rhinoclavis*, *Mamilla*, *Notocochlis*, *Uber pyriformis*, *Natica*, *Terebra affinis*, *T. muscaria*, *Oliva coerulea*, *O. erythrostoma*, *Pyramidella*, *Pagurus deformis*, *Clibanarius virescens*, *Thalamita admete*, *Penaeus*, *Calappa hepatica*, *C.* sp., *Portunus granulatus*, *Holothuria atra*, *H. arenicola*, *Actinodendron*, *Phyllodoce*, *Gorgonorhynchus*, *Melo*	*Eurythoë* *Balanoglossus* *Mesochaetopterus* *Codakia* *Solemyarina* *Regozara* *Tellina* *Lioconcha* *Holothuria arenicola* *Glycera* "*Lineus*" sp. *Ophichthys*

shingle, and the unidentified anemone found was equally common in crevices between oysters on the beach rock.

(4) *Clean Sand* (VII, XXX, XXXVII).—Only in XXX (sandy glade) were there species whose presence is possibly related to the proximity of mangroves. These are: *Atrina*, common near mangroves but not elsewhere; *Holothuria scabra*, which apparently prefers sheltered conditions, slight muddiness, and the presence of *Zostera* or *Thalassia*; *Clibanarius padavensis*, which overlapped into the adjacent sand; *Myrionema*, typically on mangrove roots, but here common on occasional stones; *Thalassia* and *Halophila*; *Thalamita crenata*, which apparently prefers semi-muddiness and an abundance of shallow water retreats; *Scylla*, whose presence was indicated by occasional burrows.

The faunas of the remaining localities resemble those of the sandy moats (Section VI(*d*)(ii)).

TABLE 8

FAUNA ON BOULDERS ON THE STONY FLAT (XXII) AND IN MOATS

Ecological Significance	Level in Relation to Moat Level (M.L.)		
	1 ft Above to Nearly M.L.	Just Above to M.L.	M.L. and Below
Dominant	*Siphonaria zanda* *Onchidium verruculatum*	*Chama*	*Tridacna crocea*
Subdominant or very common	*Acanthozostera*	*Perna* *Spondylus*	*Trochus obeliscus*
Common or present	*Trochus obeliscus*	*Trochus obeliscus* *Navicula*	*Navicula* *Tetraclita vitiata*

(*b*) *The Sand Flat* (Plate 5, Fig. 2)

Two areas were distinguished: (i) a smaller area of surface rubble and stones near the south-east of the sand cay; (ii) a larger sandy area which merged into the stony flat.

(i) *Rubble Area* (XIX(*c*); Table 7).—Although the substratum consisted chiefly of rubble, a few rubble-free patches of *Thalassia* and *Halophila* occurred. The presence of three *Rhizophora* seedlings was noted. Three habitats were studied: on the surface, under non-embedded stones, and under stones embedded in sand. The fauna under embedded stones resembled the infauna of purely sandy areas in the dominance of *Ptychodera* and *Edwardsia* spp.

(ii) *Main Flat* (XIX(*d*), XX, XXI, XXIII; Table 7).—No faunistic heterogeneity could be detected, despite the occurrence of higher areas forming minor sand-banks and lower areas dominated by *Thalassia*, *Halophila*, and *Padina*.

The surface fauna was characterized by the abundance of carnivorous gastropods and crabs. This fauna overlapped into the stony flat, where two additional species

(*Strombus luhuanus* and *Lambis*) were found. Towards the anchorage *Laganum depressum* was an additional and common species.

(*c*) *The* Thalamita *or Stony Flat* (XXII; Plate 6, Fig. 1)

This was typically just below moat level, and characterized by flat slabs of dead coral (*Acropora*), interspersed with horseshoe clams (*Hippopus*) and occasional coral boulders. Between these the surface consisted of coral rubble carrying a dense algal cover ("*Sargassum*", *Turbinaria*, *Padina*, *Halimeda*) and sand carrying *Thalassia* and *Halophila*.

TABLE 9

COMMONER ANIMALS UNDER STONES AND BOULDERS, THALAMITA FLAT (XXII)

Within each group, the arrangement is roughly in order of abundance

OPHIUROIDEA	CRUSTACEA
Macrophiothrix	*Leptodius*
Ophiarthrum elegans	*Phymodius*
Ophiolepis	*Atergatis*
Ophiarachnella septemspinosa	*Thalamita stimpsoni*
Ophiarthrum pictum	*Pagurus megistos*
ECHINOIDEA	*Gonodactylus*
Echinometra	*Actaea hirsutissima*
Diadema	*Euxanthus*
HOLOTHURIOIDEA	*Pagurus fabimanus*
Holothuria impatiens	*Eupagurus*
H. leucospilota	MOLLUSCA
Synapta	*Promantellum*
Stichopus chloronotus	*Arabica*
S. variegatus	*Anomia*
ASTEROIDEA	*Pinctada*
Nardoa pauciforis	*Dolabella*
Linckia	*Darioconus*
	Turbo nivosus

Three habitats were distinguished:

(1) On the submerged rubble and sand. The fauna of this habitat resembled that of comparable situations in the moats, and is dealt with later (Tables 11 and 12).

(2) On emergent stones, boulders, or *Hippopus* shells. The fauna (Table 8) showed three zones: *Siphonaria–Onchidium*, *Chama*, and *Tridacna*. The first two showed resemblances to the beach rock and the last to the boulder zone (Section VII(*b*)).

(3) Under boulders and stones. Again the fauna resembled that of the moats, but was more accessible and richer on the stony flat, and is here considered (Table 9).

Echinoderms, especially brittle stars, and crustaceans were prominent. The abundant sponge, polychaete, and polyzoan faunas were not collected. (Stephenson *et al.* (1931, p. 54) record 13 species of sponges from this habitat.)

TABLE 10

MOAT CORALS ARRANGED IN ORDER OF FREQUENCY OF OCCURRENCE

Symbols indicative of abundance relate only to the coral population and not to the total population, as follows: × × × × ×, dominant; × × ×, co-dominant; × ×, subdominant or very common; ×, common; P, present; v.c., very common

Species	VII 1½ ft Moat: west *Porites* pond, very extensive	XXVIII 1 ft Moat: madrepore, extensive drainage	XVII 6 in. Moat: northern extensive	XXXVII 1 ft Eastern drainage creek from mangroves, extensive	XXXVI 1 ft Moat: end of eastern drainage creek, extensive	VIII 1 ft Moat: lone mangrove, extensive	XXX 9 in. Mangrove area and sandy glade, extensive	XXII 6 in. Stony flat, extensive	XXVII 4 in. *Montipora* lawn, drainage	XXXII 6 in. Moat: near *Ceriops* thicket, small	Total No. of Occurrences	Summated No. of Symbols of Abundance†
Montipora divaricata	×	× ×	P	× × ×	P	× × ×	P‡	× ×	× × × × ×		9	17½
Goniastrea pectinata	×	× × ×	× × ×	×	P	P	P	× ×	× ×		9	13½
Pocillopora damicornis	P	× ×	P	× ×	P	× × ×	P	×	× ×		9	12
Leptastrea purpurea	P	P	P	× × ×	× ×	P	P	P	× ×		9	10
Porites lutea	× × × × ×	× × ×	P		× ×	×		× × × × ×	× ×		7	18½
Platygyra	×		× × ×		× ×	P	P	P	P		7	8
Favia speciosa	×		P	P		P	P	P	P		7	4
*Porites lobata**	×	P		× ×		P	× × × × ×			× × × × ×	6	14
Favia pallida	×	× ×	P			P			P		5	4½
Favites abdita	P	× ×	P			P		P			5	4
Acropora pulchra	P	×		× ×						P	4	4
*Cyphastrea serailia**			P		× ×		P	P			4	3½
Acropora hebes	P	×				P	P				4	2½
Goniastrea retiformis	×				× ×		× ×				3	5
Fungia fungites haimei	× ×	×		P							3	3½
Symphyllia	P	P	P								3	1½
Additional spp.	*Galaxea fascicularis** *Fungia echinata* *F. actiniformis* *Parahalomitra** *Goniopora minor** *Lobophyllia corymbosa*	*Psammocora* *Hydnophora* *Cyphastrea microphthalma** *Pavona decussata* *Acropora squamosa* *Heliopora*	*Montipora* sp. 1 *Montipora* sp. 2 *Favites complanata** *F. virens**	*Millepora exaesa* (v.c.) *Acropora corymbosa* (v.c.) *A. latistella* (v.c.)* *Acropora* sp. (v.c.)* *Coscinaraea**	*Favites aspera* (v.c.)* *Leptoria* *Galaxea fascicularis*		*Leptastrea transversa**		*Leptoria*			
Total number of spp.	21	18	15	13	11	11	11	9	9	2		

*Species not previously recorded from the moats.
†P taken as one-half.
‡Recently dead.

(*d*) *The Moats*

Apart from the moats proper, many areas within the ramparts remained covered at low water, and showed sufficient faunistic similarity to the moats to be included under this heading. Collections were made from six true moats (VII, VIII, XVII, XXVIII, XXXIV, and XXXVI), two comparable localities on the shallower flat (XXII and XXVII), and two comparable localities adjacent to mangroves (XXX and XXXVII). The significant habitat details are given in Tables 10–12, and photographs of true moats are shown in Plate 6, Fig. 2, and Plate 7, Fig. 1.

In the "moats" as here detailed, the flora is divisible into two units: the sand-dwelling species (mainly the *Thalassia*) and the extremely varied rubble-dwelling species. The fauna can, for convenience, be divided into four units: (i) corals on the substratum; (ii) remaining fauna on the substratum; (iii) species on coral rock and associated habitats; (iv) species under stones and boulders.

(i) *Corals.*—In many areas the numbers of large, medium, and small colonies of a given species were noted but the data are unwieldy, and add little to the general picture. Instead the abundance of each species is indicated in general terms (Table 10). These terms refer to the coral population only, not to the total fauna, and are comparable only within one locality. Thus "dominant" in one locality may be equivalent in absolute density to "very common" in another.

Forty species were recorded from the moats, the number in the several localities varying from 21 to 2. In general, the specific variety was greatest in the deeper and more extensive moats, the shallow northern moat being the most conspicuous exception. Here possibly, ease of communication with the outside was significant. Another exception was the *Montipora* lawn (XXVII), where distinct drainage at low water was apparently responsible for increased density and variety. Drainage seemed to have similar effects in other localities (e.g. XXVIII, madrepore moat; XXXVII, eastern drainage creek).

The most characteristic moat species in 1954 were the first eight listed in Table 10, which comprise six robust and two fragile species. Most of the former were large masses, and had evidently survived the 1950 cyclone, while the latter were small, and had probably been destroyed and had regrown.

Of the robust species, *Porites lutea* was dominant in the deeper moats, and had formed micro-atolls (Plate 7, Fig. 1). It was accompanied by *Goniastrea pectinata*, which itself became dominant in moats of intermediate and shallow depths. Here both *Platygyra* and *Favia speciosa* became important. *Porites lobata* and *Leptastrea purpurea* were generally distributed.

Of the fragile species, *Montipora divaricata* was abundant, and formed beds or "lawns" in shallow water. *Pocillopora damicornis* was more widespread but never as dense.

The conspicuousness of fungids merited attention. However, only in the *Porites* pond (VII) were they very common, although *Fungia fungites haimei* was common in the *Fungia* moat.

Many of the moat species were common outside the ramparts, and were probably "overlaps" therefrom. These include *Acropora pulchra*, *A. squamosa*,

TABLE 11

RUBBLE-DWELLING SPECIES OF THE MOATS, ARRANGED IN ORDER OF FREQUENCY OF OCCURRENCE

Symbols indicative of abundance as in Table 10. These refer to the habitat as a whole and not merely to the rubble-dwelling species

Species	XVII 6 in. Northern moat, rubble	XXXVII 1 ft Drainage creek from eastern mangroves, part rubble, part sand	XXVII 4 in. *Montipora* lawn, rubble	XXII 6 in. Stony flat, rubble	VIII 1 ft Lone mangrove, mostly sand	XXVIII 1 ft Madrepore moat, rubble	XXXVI 1 ft Eastern moat, part rubble, part sand	VII 1½ ft Western *Porites* pond, rubble	XXXII 6 in. Near *Ceriops* thicket, rubble	XXX 9 in. Sandy glade, sand	Total No. of Occurrences	Summated No. of Symbols of Abundance‡
*Diadema**	×	× × × × ×		×	×	×	P	× × × × ×	×	×	9	16½
Hippopus		P	×	× ×	×	P	P		×	× ×	8	8½
Synapta†	×	P			P			P	×	×	6	4½
Echinometra†		P	P	×		×	P		×		6	4½
Stichopus chloronotus	×		×		×	×		P			5	4½
Linckia	×		P	×							3	2½
Tridacna fossor	P	×			×						3	2½
Pinctada			P	×		P					3	2
Cypraea		P			P			P			3	1½
*Lambis**		P				P	P				3	1½
Additional spp.	*Sarcophyton* (× × ×) *Holothuria coluber* (×)† *Sinularia polydactyla* (×) *Lobophytum crassum* (×) *L. pauciflorum validum* (×) *Nephthea* (×) *Nardoa pauciforis* (×) *Gonodactylus* (×) *Sinularia flexibilis* (×) *Pagurus deformis* (P)* *Trochus niloticus* (P)	*Culcita* (P)* *Conus capitaneus* (P)	*Nardoa pauciforis* (P) *Gonodactylus* (P) *Pagurus deformis* (P) *Trochus niloticus* (P)	*Strombus luhuanus* (× ×) *Atergatis* (× ×)† *Arabica* (P) *Ophiarachna* (P)†	*Holothuria impatiens* (P) *Tripneustes* (P)	*Turbo nivosus* (P)†	*Zoanthus* (× × × × ×) *Aplysia* (P) *Palythoa* (P)	*Polyplectana* (P)	*Monetaria annulus* (×)	*Monetaria annulus* (×)		
Total number of spp.	16	9	9	9	8	7	7	5	5	4		

*Species occurring equally on rubble or sand.
†Species typically associated with stones.
‡P taken as one-half.

TABLE 12

SAND-DWELLING SURFACE SPECIES OF THE MOATS ARRANGED IN ORDER OF FREQUENCY OF OCCURRENCE

Symbols indicative of abundance as in Tables 10 and 11. These refer to the habitat as a whole and not merely to the sand-dwelling species

Species	XXX 9 in. Sandy glade, sand	XXXVI 1 ft Eastern moat, part sand, part rubble	XXXVII 1 ft Eastern drainage, part sand, part rubble	XXII 6 in. Stony flat, rubble	XXVII 4 in. *Montipora* lawn, rubble	XXXII 6 in. Near *Cerious* thicket, rubble	XVII 6 in. Northern moat, rubble	XXVIII 1 ft Madrepore moat, rubble	VII 1½ ft Western *Portes* pond, rubble	VIII 1 ft Lone mangrove, sand	Total No. of Occurrences	Summated No. of Symbols of Abundance†
Marginopora	× ×	×	×	×	×	×	×	×	×	× ×	10	12
Holothuria atra	× ×	×	×	×	×	×	×	×	×	×	10	11
*Diadema**	×	P	× × × × ×	×		×	×	×	× × × × ×	P	9	16½
Holothuria leucospilota	× ×	P	P	×	P	×					7	6
Isognomon	× ×			×	P	×					4	4½
*Lambis**		P	P					P			3	1½
Stoichactis		P					P	P			3	1½
Tethya	× ×					× ×					2	4
Actinodendron	× ×				P						2	2½
Nassarius lurida	× ×	P									2	2½
Phos	× ×	P									2	2½
Additional spp.	*Holothuria scabra* (× ×) *Atrina* (P) *Strombus gibberulus* (P)		*Culcita* (P)* *Stichopus variegatus* (P)	*Strombus luhuanus* (× ×) *S. gibberulus* (×)	*Pagurus deformis* (P)		*Pagurus deformis* (P)		*Actinopyga* (P)			
Total number of spp.	12	8	7	7	6	6	5	5	4	4		

*Species occurring equally on rubble or sand.
†P taken as one-half.

Symphyllia, *Galaxea fascicularis*, *Lobophyllia corymbosa*, unidentified species of *Montipora*, and *Favites virens*. One locality (XXXVII) in the eastern drainage creek is of special interest in this respect. Here *Acropora* colonies were flourishing, and were not attached to the substratum but merely embedded in sand and rubble. Fragments had evidently been washed in, had survived, and flourished. Fragments were being washed into the southern moats in August 1954.

(ii) *On the Substratum.*—In every moat, rubble and sand were mixed in varying proportions. The fauna of rubble was broadly distinguishable from that of sand, and their distributions are given in Tables 11 and 12. The fauna of living coral, including commensals, was not investigated.

Rubble species (Table 11) totalled 33, and included five typical of mixed substrata of sand and rubble, and six partly associated with stones. The elongate holothurian *Synapta* is typical of this last group with its aboral end under a stone, and its body extended over gravel. Echinoderms were conspicuous both for density and variety, and the abundance of *Diadema* is indicated by Plate 7, Figure 2. Molluscs were obvious, especially *Hippopus*, which was widespread and common on the shallow margins of the moats. Coelenterates, other than hard corals, were patchily distributed, and dominated certain small areas of coarse rubble coated with a brown algal felting. In the northern moat at least four genera of soft corals occurred, whilst in the eastern moat *Zoanthus* was dominant, with occasional patches of *Palythoa*. *Zoanthus* was so inconspicuous in retraction that it may have been overlooked at other localities, including mangrove roots (see Stephenson *et al.* 1931, Plate XXI, Fig. 4). The remaining species included crustaceans which typically live under stones (e.g. *Pagurus deformis*, *Atergatis*, and *Gonodactylus*).

Sand species (Table 12) totalled 19, including five previously listed. In the sandiest of the "moats", the sandy glade (XXX), 11 of 15 species of the surface fauna were sand-dwelling species, but elsewhere the proportion was lower.

Three species, *Nassarius lurida*, *Phos rufocinctus*, and *Strombus gibberulus* were typical of situations just exposed at low water, and may be regarded as sand-flat species "overlapping" into the sandy moats.

The sand, like the rubble, carried a conspicuous echinoderm fauna in which the most widespread and obvious species were *Holothuria atra* and *H. leucospilota*.

Whenever conditions were moderately stable *Thalassia* occurred, and carried a dense population of *Marginopora*. In many areas *Marginopora* was possibly the dominant animal, and its significance may not be indicated adequately in Table 12.

(iii) *Coral Rock and Associated Habitats.*—Small coral boulders occurred in the moats as on the stony flat, and faunistic details have already been given (Table 8).

When the massive corals reach moat level, the tops evidently die and produce a flat rock surface. This carried a fauna with *Chama* dominant and *Spondylus* very common, which resembled the beach rock fauna at the same level (Table 3). Smaller numbers of species are explained by the isolation of the habitat.

In the shallower moat situations, for example, the northern sides of the western, *Fungia*, and madrepore moats, the flat dead tops of corals covered much of the moat surface (Plate 8, Fig. 1). By an extension of this cover an almost continuous flat

pavement would be produced, with small cavities containing the remnants of growing corals. This situation existed on the borders of the mangrove park (XXIX) in the form of "honeycomb rock" with the interstices partially sand-filled. Between the rocks, in a few inches of water, there was a surprisingly varied fauna on the sand and rubble (Table 13, column 2), resembling that of the moats (Table 12).

At one locality (VI) flat rock, presumably derived as explained above, existed at a higher level, viz. about 3–4 in. above the present moat level. The under-rock fauna resembled that of the rubble areas of the sand flat with admixture of rock-dwelling species (e.g. *Trochus* spp.). The sparse fauna on the surface sand between rocks was dominated by species characteristic of the stony margins of the sand flat (Table 13, column 1).

TABLE 13

FAUNA OF SHALLOW SANDY AREAS NEAR CORAL ROCKS WITHIN THE RAMPARTS

Ecological Significance	*Chama* Bed (VI) Mostly on sand 3–4 in. above moat level	Honeycomb Rock (XXIX) On sand and rock 2–3 in. below moat level	*Chama* Bed (VI) Under rocks amongst sand 2–3 in. above moat level
Dominant	*Holothuria atra*	*Holothuria leucospilota* *H. atra*	*Strombus gibberulus* *Clibanarius virescens*
Subdominant or very common	*Marginopora*	*Marginopora* *Hippopus* *Isognomon*	*Uber pyriformis* *Thalamita admete*
Common or present	*Strombus luhuanus* *S. variabilis* *Hippopus* *Stoichactis*	*Atergatis* *Lambis* *Actinodendron* *Stoichactis* *Pinctada* *Actinopyga* *Holothuria coluber* *Stichopus variegatus* *Nassarius coronatus* *Niotha*	*Ophiarachnella* *Trochus obeliscus* *T. niloticus* Porifera (3 spp.)

(iv) *Under Stones and Boulders.*—The under-stone fauna of the moats proper was itself similar to that of the *Thalamita* flat, as already listed, and only comparison is necessary. Species recorded from the *Thalamita* flat but not from the moats comprised: *Ophiarthrum pictum*, *Stichopus chloronotus*, *Thalamita stimpsoni*, *Pagurus megistos*, *Nardoa pauciforis*, *Anomia* sp., and *Dolabella*. Conversely, species recorded only from the moats comprised: *Cryptophallus* and *Euplana* (both new records of Australian Polycladida), hydroids, *Ophiarachna*, *Holothuria martensii*, *Chama*, *Haliotis*, *Ophiocoma erinaceus*, *Ophiomastix*, *Abudefduf*, and *Hemiscyllium*.

Most of the differences from the moat fauna are among the less common species, and probably represent "sampling errors". Some (e.g. the presence of the fishes

TABLE 14

FAUNAS OF UNCONSOLIDATED ("LOOSE") SHINGLE AT DIFFERENT LEVELS ON THE NORTH OF THE ISLAND

Ecological Significance	0 M.H.W. Loose white shingle	I H.W.N. Loose brown shingle	II M.S.L. Brown shingle, gritty sand 1½ in. down	III L.W.N. Alga-covered shingle with stones	XVI M.L.W. "Dirty" alga-covered shingle, surface fauna	M.L.W. to L.W.S. Subsurface fauna
Dominant	Nil	*Planaxis*	Talitridae*	*Petrolisthes* *Clibanarius virescens*	*Zoanthus**	*Zoanthus**
Subdominant or very common		Talitridae*	*Petrolisthes* *Cerithium jannelli* *Nerita* spp.	Talitridae* Collembola* *Macrophiothrix*	*Sarcophyton* *Sinularia variabilis* *Lobophytum crassum*	
Common or present		*Metapograpsus*	*Clibanarius virescens* *Morula margariticola* *Onchidium verruculatum* *Polycheira* *Leptodius* *Metapograpsus* *Salarias*	*Chlorodopsis* Anemone *Thalamita admete* *Macrophthalmus quadratus* Polychaeta (3 spp.) *Asaphis* *Actaea tomentosa* *Etisus*	*Hippopus* *Echinaster* *Stichopus chloronotus* *Linckia* *Nardoa pauciforis* *Atergatis* *Platygyra* *Symphyllia* *Leptastrea purpurea* *Favia speciosa*	*Conus capitaneus* *Thalamita prymna* *T. coeruleipes* *Turbo nivosus* Porifera (at least 5 spp.) *Torinista* *Ophiocoma scolopendrina* *Salmacina* Hydroida *Haliotis* *Diadema* (juv.) *Asterope*

*Inconspicuous species, liable to be overlooked.

Abudefduf and *Hemiscyllium* in the moats) are due to the fact that deeper water occurs in the moats.

VII. The Shingle Ramparts and Boulders

(*a*) *Shingle*

Shingle had been thrown up round the island to form ramparts which sloped gradually seawards but terminated abruptly on their inner or moat margins. On the east side the rampart system was complex, and Fairbridge and Teichert (1947) noted that the 1934 cyclone had so altered the system that the original concept of inner and outer ramparts no longer held. The 1950 cyclone added further complications. This mangrove–shingle region, corresponding to the "inner ramparts" of Stephenson *et al.* (1931), has been dealt with in Section VI(*a*)(i).

The remaining shingle structures have also changed. Thus Fairbridge and Teichert (1947) noted a southerly extension of shingle which was encroaching upon the "*Tripneustes* spit" of the key chart of Stephenson *et al.* (1931). In 1954 this extension was more marked (Plate 7, Fig. 1).

The amount of shingle on the seaward side of the ramparts seemed related to wave action. Thus on the exposed eastern and south-eastern sides, there was little or no loose shingle from H.W.N. to below L.W.S. Between these levels the substratum consisted of semiconsolidated shingle or "crumbly" beach rock (Plate 8, Fig. 2). This seemed to represent the deeper layers of normal shingle, the surface layers having been removed by cyclonic action. Only on the northern side of the island, where conditions were more sheltered, did loose shingle extend down to L.W.S.

In loose shingle it was rarely possible to separate the surface and subsurface faunas. They are probably identical, and were normally collected just below the surface, where the maximum concentration occurred.

(i) *Effect of Level, Loose Shingle.*—On the eastern side of the anchorage, loose shingle extended from M.H.W. to L.W.N., and collections were made from a series of localities (0, I, II, III). Below L.W.N. reasonably loose shingle only occurred on the western side of the anchorage (XVI). The five localities are here considered as a continuous series.

There were three inconspicuous zones: downwards to H.W.N., white shingle without animals (0); H.W.N. to M.S.L. or slightly lower, brown shingle with algal encrustation (I, II); and L.W.N. or slightly higher to L.W.S., tufted algae, with *Gelidium* the most obvious genus (III).

The most significant faunistic features (Table 14) were: the increase in specific variety as the shingle beaches were descended (below M.L.W. the richness of the fauna approached that of the moat rubble); the occurrence of several animals not collected in the moats (e.g. *Thalamita* spp., *Conus capitaneus*); the abundance of soft corals (this was a feature of the anchorage as a whole, and another point of difference from the moats); the abundance of inconspicuous species (e.g. talitrids

and *Zoanthus*).* Further, the tolerably distinct successional zoning animals (*Planaxis*, *Petrolisthes*, *Clibanarius virescens*, and soft corals), were not restricted to shingle, and the first three were equally, or even more common, on or under beach rock (Tables 3, 4), whilst the soft corals also characterized dead coral masses in the anchorage.

TABLE 15

FAUNA OF SHINGLE WITH GRITTY SAND AT *c.* M.S.L.

Ecological Significance	II Loose surface shingle, gritty sand below; sheltered	XXXI(2) Loose semiconsolidated sandy shingle; exposed	XXXII Compacted but non-consolidated sand, grit and shingle; sheltered
Dominant or codominant	Talitridae	*Onchidium verruculatum* *Nerita* spp.	*Nerita planospira*
Very common	*Petrolisthes* *Cerithium jannelli* *Nerita* spp.	*Cerithium jannelli*	*N. polita* *Clibanarius virescens* *Modiolus*
Common	*Clibanarius virescens*	*Metapograpsus*	*Cerithium jannelli*
Present	*Morula margariticola* *Onchidium verruculatum* *Polycheira* *Leptodius* *Salarias* *Metapograpsus*	*Morula margariticola* *Acanthozostera* *Emarginula* *Discucumaria* *Chione* *Eunice* Syllidae (1 sp.) Sipunculoidea (2 spp.) *Thalamita admete* *Gonodactylus* *Leptodius*	*Onchidium verruculatum* *Pollia*

The above faunistic picture seemed typical of non-consolidated shingle right round the island. Thus the uppermost white shingle on the eastern side, like locality 0, was devoid of animals. Brown shingle at H.W.N. had throughout a fauna similar to that of 1 (Plate 9, Fig. 1). For example, at XXXI(1) on the south-east side of the island, the only apparent differences were that *Quoyia* was very common, probably as an "overlap" from the mangrove shingle, and *Acanthozostera* was present, probably as an "overlap" from adjacent, more consolidated localities. Much the same applies at M.S.L. For example, at the clam spit (XXV) the only differences were that *Onchidium* was common, not merely present; *Clibanarius virescens* was more common than *Petrolisthes;* and there were differences in the minor species, e.g. *Schizochiton* and xanthids.

*Because of the inconspicuousness of such species the possibility exists that their abundance at each level was not accurately noted, and the characteristic species at the different levels listed in Table 14 can only be designated as the commonest *obvious* species.

(ii) *Effects of Admixture of Sandy Grit and Degree of Compacting of the Environment.*—In the previous series, at one locality (II, at M.S.L.) gritty sand occurred below the surface but had no detectable effect on the fauna other than the addition of the holothurian *Polycheira*. On the eastern side of the island there were two localities (XXXI(2) and XXXII) at a similar level (M.S.L.) in which surface grit was present. This grit, by filling interstices, produced more compact environments. Comparison of these three localities (Table 15) shows its effect. The environments also differ in the degree of lithification (see Section VII(*a*)(iii)).

In general, a talitrid–*Petrolisthes* community in loose environments was replaced by a *Nerita* community in more compacted situations, where far fewer species were

TABLE 16

FAUNAS OF LOOSELY CONSOLIDATED, AND ALMOST SOLIDLY CONSOLIDATED SHINGLE ON EAST SIDE OF THE ISLAND, AT M.S.L.

Ecological Significance	XXXI(2) Loosely consolidated, rough surface, inconspicuous algal film	XL Consolidated, smooth surface, alga-covered
Dominant or codominant	*Onchidium verruculatum* *Nerita* spp.	*Planaxis* *Turbo porphyrites*
Very common	*Cerithium jannelli*	*Nerita annulata* *Onchidium verruculatum*
Common	*Metapograpsus* Brown anemone	*Metapograpsus* *Cerithium dorsuosum* *Petrolisthes* Anemone
Present	*Emarginula, Morula margariticola, Acanthozostera, Chione, Discucumaria, Eunice* sp., Syllidae, Sipunculoidea (2 spp.), Porifera, *Thalamita admete, Gonodactylus, Leptodius*	*Morula marginalba, Gonodactylus, Leptodius, Trochus obeliscus, Polycheira, Phyllodoce, Nereis*

present. The looser environments probably provided moving space for a reasonably rich crab fauna in one case (II) and for a still richer one, with added polychaetes, in another (XXXI (2)).

(iii) *Effect of Lithification.*—On the east of the island, surface shingle was apparently removed by the 1950 cyclone. In some places the bared surface consisted of shingle and grit, partly lithified into loose aggregates, and in others of an almost consolidated rock (Plate 8, Fig. 2). The latter carried a denser algal cover (including "lithothamnion") than the former, and this may have led to further differences between the extremes.

The faunas of habitats with different degrees of lithification were compared at two levels, M.S.L. and L.W.N. At M.S.L. (Table 16) the *Onchidium–Nerita* community of the looser environment was replaced by a *Planaxis–Turbo* community

on the more consolidated. The richer fauna of less important species in the former was no doubt due to its more open texture, but there were numerous species common to both enviroments.

At L.W.N. (Table 17) the degree of consolidation of the substratum had profound faunistic effects. In the looser aggregates *Clibanarius virescens* predominated as in loose shingle, but with a richer accompanying fauna, presumably owing

TABLE 17

FAUNAS OF SHINGLE CONSOLIDATED TO DIFFERENT DEGREES ON EAST SIDE OF THE ISLAND AT L.W.N.

Ecological Significance	XXXI(3) Soft, semiconsolidated, pitted, algae poorly developed	XXXIII(1) Fairly hard, rough-surfaced ("honeycombed"), lithothamnion moderately well developed	XL Hard, smooth, brown algae conspicuous
Dominant or codominant	*Clibanarius virescens*	*Monetaria annulus*	*Modiolus agripeta*
Subdominant	*Nerita albicilla*	*Ophiocoma scolopendrina*	Nil
Very common	*Dynamena* *Nerita annulata*	Porifera, Polyzoa, *Clibanarius virescens,* *Macrophiothrix, Ophiactis,* *Dynamena*	Nil
Common	*Nerita planospira* *Siphonaria zanda* *Acanthozostera*	*Conus marmoreus*	Nil
Present	*Trochus obeliscus* *Macrophiothrix* *Echinometra* Porifera *Saron, Petrolisthes* *Atergatis* Sipunculoidea (1 sp.) *Morula margariticola* *Holothuria impatiens* *Navicula, Periglypta* *Elamena, Echinoneus*	*Conus marmoreus, Holothuria leucospilota, Echinometra, Promantellum, Navicula, Discucumaria, Mancinella, Diogenes, Nerita albicilla, Atergatis, Montipora divaricata* (in pools), *Gonodactylus, Chlorodopsis, Elamena, Pollia*	Nil

to the abundance of permanent crevices. As against this, in the fairly hard rock the cowrie *Monetaria annulus* predominated (Plate 9, Fig. 2). The honeycombed nature of the rock again allowed of a varied accompanying fauna. On the hardest rocks *Modiolus agripeta* were completely dominant (Plate 10, Fig. 1). There was no obvious resemblance to the fauna of beach rock, possibly because no crevices were left for other sizable animals.

On the east of the island the substratum between H.W.N. and L.W.N. was a mosaic of areas dominated by one or other of the groups listed. Presumably, with

increasing recovery from cyclones there would be increasing consolidation of shingle, and if so, many of the animals listed may only be temporary inhabitants. Other species, for example *Modiolus*, might spread and form the climax to a faunistic cycle. If so, it is surprising that the mussel beds were not recorded during the 1928–9 survey, when stability should have been attained. That this was probably an oversight is indicated by Iredale's (1939) comment on the species: "a littoral species living at Low Isles near the outer edge, where in places, it is very abundant, forming a mat, apparently always gregarious".

Against this concept of increasing stabilization there is a possibility that shingle accumulates on the slope during calm weather.

TABLE 18

FAUNA ON THE BOULDERS OF BOULDER TRACT (XXIV)

Ecological Significance	H.W.N. to L.W.N.	L.W.N. to M.L.W.	M.L.W. to E.L.W.S.
Dominant	*Crassostrea amasa*	*Acanthozostera*	*Tridacna crocea*
Subdominant or very common		*Tetraclita vitiata* *Crassostrea amasa*	
Common or present	*Planaxis* (near H.W.N.) *Acanthozostera* *Tetraclita vitiata* *Siphonaria zanda* *Perna* Vermetidae (1 sp.)	*Chama* *Tetraclita coerulescens* *Perna*	*Acanthozostera* *Siphonaria* *Palythoa** *Sarcophyton** *Sinularia* spp.*

*Patches.

(*b*) *Boulders*

Boulders were sparsely scattered over the flat and moats (for fauna see Table 8), and on the eastern side of the anchorage, but were most conspicuous as a boulder tract to the west of the cay. Those corresponding with the boulder zone of the 1928–9 survey had been almost entirely removed from the relatively wave-lashed southern and eastern slopes.

At the boulder tract (XXIV), the environment resembled the beach rock, but was more vertical, more exposed to wave action, and further removed from the abrasive action of the sand. Attention was focused on the surface fauna rather than the borers, which have been described by Otter (1937), and was further restricted to a level not lower than E.L.W.S., below which the environment merges with the seaward slopes. Three zones were visible: oyster, "bare", and *Tridacna*, and their respective faunas are listed in Table 18.

The oysters were denser on the boulders than elsewhere at Low Isles, and probably the densities of other animals were reduced through restriction of available

space. The "bare" zone was dominated by *Acanthozostera*, whose abrasion marks were evident. This abrasion may delimit the lower border of the oyster zone, and seems responsible for the removal of rock from the boulders. At the bare zone the boulders were deeply incurved to form a central waist which was occasionally

TABLE 19

CORALS OF SHALLOW WATER IN OR NEAR THE ANCHORAGE

Size	XVI M.L.W.	XVIII M.L.W. to L.W.S.	V L.W.S. to 1 ft below	XVIII L.W.S. to 1½ ft below
Large corals			*Symphyllia*	*Symphyllia* *Porites lutea* *Parahalomitra*
Medium-sized corals		*Acropora squamosa*	*Symphyllia* *Lobophyllia corymbosa* *Acropora pulchra* *A. squamosa*	*Herpolitha*
Small corals	*Platygyra* *Symphyllia* *Leptastrea purpurea* *Favia speciosa*	*Acropora pulchra* *A. hebes* *Leptastrea purpurea* *Favia pallida* *F. speciosa* *Porites lutea* *Pocillopora damicornis* *Favites abdita* *Galaxea fascicularis*	*Acropora hebes* *Leptastrea purpurea* *Goniastrea pectinata* *A. squamosa* *Pocillopora damicornis* *Favites abdita* *Galaxea fascicularis* *Porites lutea* *Platygyra* *Goniastrea retiformis* *Fungia fungites haimei* *Favia pallida* *Cyphastrea serailia*	*Fungia fungitis haimei* *Galaxea fascicularis* *Symphyllia* *Lobophyllia corymbosa* *Acropora squamosa* *Porites lutea* *Favia pallida* *Montipora* spp. *Goniastrea pectinata* *Polyphyllia* *Pavona* (*Polyastrea*) *obtusata* *Acropora exilis* *Oxypora* *Fungia echinata* *F. horrida* *Acropora pulchra* *A. hebes* *Millepora* *Cyphastrea serailia* *Goniopora* *Porites andrewsi* *Favites halicora*
Total No. of spp.	4	10	*c.* 16	*c.* 25

perforated (Plate 10, Fig. 2). It seems likely that many boulders noted in 1928–9 have subsequently been cut through at their central waists, the top portions having then fallen to lower levels and been converted into stones dominated by *Tridacna crocea*. These bivalves are abundant in both boulders and stones, but apparently cause only slow destruction of the rock.

On the eastern side of the anchorage, the small boulders were more sheltered than those of the boulder tract and their surfaces were covered by encrusting algae. A detailed faunistic account is omitted; the significant differences from the boulder tract are: the replacement of a distinct oyster zone with a mixed population of oysters, *Tetraclita vitiata*, *Patelloida*, and *Acanthozostera;* the presence of *Zoanthus* at about M.W.L.; the dominance of algae (especially *Turbinaria* and *Dictyosphaeria*) at about L.W.S. on the rocks containing *Tridacna crocea*.

VIII. The Seaward Slopes and Anchorage

These environments were taken as the region round the perimeter of the island lying below M.L.W. In the trickle areas, where water drains from the moats, there are environments above M.L.W. with faunistic affinities with the seaward slope, and these are also considered below.

Collections were made from the upper levels of hard coral growth to about 2 ft below L.W.S. Below this level, surf hampered observations except in the anchorage, where calm conditions prevailed generally.

(*a*) *Corals*

The multiplicity of species was such that it was difficult to arrange them in the usual degrees of ecological dominance. Throughout, observations were made of the relative sizes of corals.

The localities collected from are divisible into five series:

(i) The anchorage and north of the cay (V, XVI, XVIII): substratum, at levels collected from, of dead hemispherical corals, stones, and rubble; considerable shelter; soft corals abundant, hard corals sparse (Table 19).

(ii) The north-eastern side of the island (IX): substratum rock, rubble, and gritty sand; moderate exposure to wave action; soft corals common, hard corals sparse (Table 20, columns 1 and 2).

(iii) The south-eastern side (XXXIII): substratum consolidated rock, overlain with rubble and gritty sand at L.W.S.; exposure to wave action at a maximum, sand stirred up by breakers at L.W.S.; no soft corals, hard corals moderately common (Table 20, columns 3–5).

(iv) The eastern side (XXXV): general conditions as (iii), but continuous moisture from drainage trickle from the eastern moat; hard corals common (Table 21).

(v) The south-western side (XI, XII, XIII, XIV) as (iv), but drainage trickle from the southern moats; exposure only moderate; hard corals very common (Table 22).

On the south-western side (Table 22; Plate 11) corals were much more common than elsewhere, and there was a greater variety of species, particularly fragile species. An indistinct zonation occurred with the sequence of dominant forms: *Acropora pulchra–Montipora divaricata; Acropora pulchra–A. hebes; A. pulchra–A. exilis;* and finally *Porites lutea–Goniastrea* sp.

The first and second zones were atypical in being elevated by water drainage from the moats, the first zone being slightly above M.L.W. In the lowest zones (about

TABLE 20

CORALS OF MODERATELY EXPOSED AND FULLY EXPOSED LOCALITIES ON EAST SIDE OF THE ISLAND

Size	IX (Exposure Moderate)		XXXIII (Fully Exposed)		
	L.W.S.	2 ft below L.W.S.	Pools at L.W.N.	M.L.W.	L.W.S.
Large corals	*Symphyllia* *Goniastrea retiformis* *Porites lutea*	*Symphyllia* *Porites lutea* *Goniastrea retiformis** *Millepora tenera**			*Goniastrea pectinata** *G. retiformis**
Medium-sized corals	*Acropora squamosa* *Symphyllia* *Goniastrea retiformis* *Porites lutea* *Lobophyllia hemprichi*	*Millepora platyphylla*		*Montipora divaricata**	*Acropora humilis*
Small corals	*Leptastrea purpurea* *Favia pallida* *Goniastrea pectinata* *Acropora hebes* *Pocillopora damicornis* *Favites abdita* *Montipora tuberculosa* *Montipora* sp. *Galaxea fascicularis* *Seriatopora* *Cyphastrea serailia* *Turbinaria* *Pavona varians* *Stylophora* *Psammocora* *Merulina* *Acropora haimei*		*Montipora divaricata* *Acropora humilis*† *Favites* sp.†	*M. divaricata* *Acropora hebes* *Porites lutea* *Favia speciosa* *Goniastrea pectinata* *Leptoria* *Favites abdita* *Montipora trabeculata* *Montipora* sp.1 *Montipora* sp.2 *Favia pallida* *Goniastrea retiformis*	
Total No. of spp.	*c.* 21	5	1 + 2	12	3

*The most significant species from an ecological viewpoint.

†As detached, washed-up living fragments.

1 ft below L.W.S.) there was a marked decline in coral abundance. The fragile species were greatly affected, and massive species dominated the sparse population.

TABLE 21

CORALS, FULLY EXPOSED BUT IN A TRICKLE AREA, EAST SIDE OF THE ISLAND (XXXV)

Size	L.W.N. (sheltered pools)	M.L.W.	L.W.S.
Large corals	*Goniastrea pectinata* *Acropora hebes**	*Goniastrea pectinata**	*Goniastrea pectinata**
Medium-sized corals	*Montipora divaricata** *Montipora solanderi* *Montipora* sp. *Goniastrea pectinata* *Acropora pulchra* *A. variabilis*	*Acropora pulchra* *Montipora divaricata* *A. hebes* *Goniastrea pectinata* *Montipora* spp.	*Favia pallida* *Cyphastrea serailia* *Porites lutea*
Small corals	*Montipora divaricata* *Pocillopora damicornis* *Goniastrea pectinata* *Millepora platyphylla* *Leptoria* *Platygyra* *Hydnophora* *Leptastrea purpurea* *Favia pallida* *Porites lobata* *P. lutea*	*Montipora divaricata* *Acropora pulchra* *Goniastrea pectinata* *Leptastrea purpurea* *Porites lutea* *Platygyra* *Cyphastrea serailia* *Symphyllia* *Montipora* sp. (2) *Millepora platyphylla* *Favia pallida* *Pocillopora damicornis* *Cyphastrea serailia* *Leptoria* *Psammocora* *Favites abdita* *F. aspera* *F. complanata*	*Acropora hebes* *A. pulchra* *A. intermedia* *Millepora platyphylla* *Pocillopora damicornis*
Total No. of spp.	16	19	9

*The most significant species from an ecological viewpoint.

(b) *Soft Corals*

In the anchorage soft corals were dominant from M.L.W. to at least 20 ft below L.W.S. The substratum consisted of dead corals in the form of non-moving rubble, hemispherical coral *in situ*, small coral boulders, and massive pillars arising from deeper water.

At locality V, *Sarcophyton trocheliophorum*, *Lobophytum crassum*, and *L. pauciflorum validum* were conspicuous and *Sinularia variabilis*, *S. flexibilis*, *S. polydactyla*, and *Sphaerella echinata* were very common. *Sinularia conferta gracilis* and *Sphaerella conifera* were noted but they were not as common as the other species.

TABLE 22

CORALS MODERATELY EXPOSED, TRICKLE AREA SOUTH-WEST SIDE OF ISLAND (XI TO XIV)

Size	XI L.W.N. to M.L.W.	XII M.L.W.	XIII L.W.S.	XIV 1½–2 ft below L.W.S.
Large corals				*Porites lutea** *Goniastrea retiformis** *G. pectinata*
Medium-sized and small corals	*Acropora pulchra** *Montipora divaricata** *A. hebes* *A. squamosa* *Montipora hispida* *M. erythraea* *M. informis* *M. turgescens* *M. tuberculosa* *M. foliosa* *M. spumosa* *Goniastrea pectinata* *Cyphastrea serailia* *Porites lutea* *Favites abdita* *Leptastrea purpurea* *Platygyra* *Favia pallida* *F. speciosa* *Psammocora* *Leptoria* *Millepora platyphylla* *Favites virens* *Acropora* spp. *Pocillopora verrucosa* *P. damicornis*	*Acropora pulchra** *A. hebes** *Montipora divaricata* *A. corymbosa* *A. exilis* *A. quelchi* *A. surculosa* *A. squamosa* *Montipora foliosa* *M. hispida* *M. erythraea* *M. trabeculata* *M. turgescens* *M. informis* *M. tuberculosa* *Favia valenciennesi* *F. speciosa* *Favites abdita* *F. virens* *Goniastrea pectinata* *Leptastrea purpurea* *Porites lutea* *Hydnophora* *Platygyra*	*Acropora pulchra** *A. exilis* *Goniastrea retiformis* *A. hebes* *A. rosaria* *A. microphthalma* *A. variabilis* *A. corymbosa* *A. squamosa* *A. glochiclados* *A. hyacinthus* *A. quelchi* *A. combicyathus* *A. digitifera* *Montipora hispida* *M. erythraea* *M. turgescens* *M. foliosa* *M. trabeculata* *M. informis* *M. tuberculosa* *Favia pallida* *F. speciosa* *Favites virens* *Acanthastrea* *Goniastrea pectinata* *Leptastrea purpurea* *Symphyllia* *Pocillopora damicornis* *Platygyra* *Porites lutea*	*Platygyra* *Favia speciosa* *F. pallida* *Pocillopora damicornis* *Platygyra* *Montipora turgescens* *Montipora* sp. *Acropora variabilis* *A. squamosa* *Fungia fungites* *Pocillopora eydouxi* *A. formosa* *Echinopora* *A. quelchi* *A. humilis* *A. patula* *Pavona obtusata* *Favites abdita* *F. halicora*
Total No. of spp.	26	24	30	22

*The most significant species from an ecological viewpoint. For the numerous species of minor importance, arrangement is alphabetical.

Apart from the anchorage, soft corals dominated only one other locality (IX), and here *Sarcophyton trocheliophorum* and *Nephthea mollis* were very common. They were restricted to approximately L.W.S., below which sand abrasion probably prevented their growth. This would also explain their absence or rarity from the remainder of the east and most of the south of the island. For example, soft corals were present but not common at XIV in the south-west corner.

(c) *General Invertebrates*

Two types of areas were examined:

(i) Below L.W.S. on the exposed eastern and south-western sides of the island (IX, XIV, XXXV). Here no general invertebrates were noted. This was due in part to concentration of effort upon corals, in part to the difficulties of observations in surf, and in part to the fact that the fauna undoubtedly was sparse. There was an effective absence of open crevices, and the general substratum was dominated by moving grit.

(ii) Between M.L.W. and L.W.S. around the island. Detailed results (Table 23) show a fauna of 57 species, and this number could have been greatly exceeded by including the infauna of the corals.

The marked differences exhibited by the faunas of the various localities seem due primarily to different substrata. Thus at the sheltered northern localities most species of minor significance lived under stones or in rubble, and only here was there sufficient shelter for such habitats to exist. Some species of greater significance (e.g. *Zoanthus*) were also dependent on rubble. Similarly, at localities XXXV and XII several species were associated with hard corals, whose growth was richest at these localities. A few species (e.g. *Atergatis*, *Gonodactylus*) were common to both coral-dominated and rubble-dominated areas; the provision of crevices seemed the only common factor. Yet others characteristic of the hard cemented "honeycomb rock" on the east of the island (e.g. *Monetaria annulus*, *Trochus niloticus*) also occurred, but less commonly, on the stones and boulders of the anchorage.

The more widespread species (Table 23) occurred in numerous habitats, *Tridacna crocea* and *Echinometra* being the most significant. Both are associated with coral rock, and probably assist in its destruction.

IX. Discussion

(a) *Destruction of Corals and Recolonization*

The cyclone of 1950 at Low Isles was only of moderate intensity (winds up to 50 knots), and not obviously more severe than many others which have struck the area before and since. The unusual features suggested as responsible for the damage to the island's corals were the direction (north to north-east) from which cyclonic winds lashed the island, and the heavy swell which accompanied the cyclone. Jamieson (96th Meeting, Great Barrier Reef Committee, Oct. 3, 1952) reported that prior to the cyclone there was an abundance of branching and plate-like corals on the north-east side of the island. This is in accord with the fact that the northern sector of the island lies in the lee of the dominating south-east trades, and hence would be expected to carry a more fragile population than the southern sector. A

TABLE 23

INVERTEBRATES (EXCLUDING STONY CORALS, SOFT CORALS, SPONGES, AND POLYZOA) AT M.L.W. TO L.W.S. IN THE ANCHORAGE AND ON THE SEAWARD SLOPES

Symbols of abundance in the first half of the table are: × × ×, extremely common; × ×, very common; ×, common; P, present. In the second half of the table: v.c., very common; c, common. Additional species only recorded as present are arranged alphabetically.

Species	IV+V Boulders, rubble	IX Rock, rubble, sand	XII Cemented rock, pools, trickle	XVI Alga-covered shingle	XVIII Boulders, stones	XXXIII Cemented honeycomb rock	XXXV Cemented honeycomb rock	Total No. of Occurrences	Summated No. of Symbols of Abundance*	Typical Habitat
	Exposure to waves: Sheltered	Moderate	Moderate	Sheltered	Sheltered	More than moderate	More than moderate			
	Hard coral growth: Sparse	Sparse	Dense	Sparse	Sparse	Sparse	Sparse			
Tridacna crocea	× ×	× ×	× ×	× ×	× ×		×	6	11	In dead coral rock
Echinometra	P	× ×	× ×		× ×	× ×	×	6	9½	On and under coral rock
Zoanthus sp.		× ×		× × ×	× × ×			3	8	Amongst rubble
Monetaria annulus	P		×			× × ×	× × ×	4	7½	On and under rocks
Ophiocoma erinaceus			× ×	×			×	3	4	In coral and under stones
Tridacna fossor		×	× ×					2	3	In rubble
Linckia	P			P		P	×	4	2½	On surface
Trochus niloticus			×			P	×	3	2½	Under stones
Atergatis			×	P			×	3	2½	Under stones and in coral
Hippopus				P		P	×	3	2	On surface
Additional spp.	*Macrophiothrix* (v.c.) *Amphiperas* *Ophiarachnella gorgonia* *Chama* *Conus capitaneus* *Darioconus* *Elamena* *Gonodactylus* *Holothuria argus* *H. pardalis* *Lambis* *Ophiarthrum elegans* *Pilumnus* *Ophichthys* *Stichopus chloronotus* *S. horrens* *Synapta*	*Palythoa* (c) *Amphiperas* *Holothuria coluber* *Stichopus chloronotus*	*Ophiomastix* (c) *Aplysia* *Holothuria atra* *Lambis* *Synapta*	*Salmacina* sp. (c) *Asterope* *Conus capitaneus* *Diadema* *Diogenes* sp. *Echinaster* *Haliotis* *Nardoa pauciforis* *Stichopus chloronotus* *Thalamita prymna* *T. coeruleipes* *Torinista*	*Diadema* (v.c.) *Palythoa* (c) *Fromia* *Stichopus variegata* (Collection probably incomplete)	*Holothuria leucospilota* (v.c.) *Arabica* *H. impatiens* *Lambis* *Ophiocoma scolopendrina* *Stoichactis*	*Ophiactis savignyi* (v.c.) *Calcinus gaimardi* (c) *C. laevimanus* (c) *Clibanarius virescens* (c) *Medaeus* (c) *Nardoa novaecaledoniae* (c) *N. pauciforis* (c) *Phymodius* (c) *Gonodactylus* *Navicula* *Pilumnus*			
Total No. of spp.	21	8	12	18	7	11	19			

*P taken as one-half.

cyclone from a northerly direction might well cause more damage to the island's coral than one from the south or south-east. The cause of the unusually heavy swell which accompanied the cyclone in 1950 is unexplained.

Mechanical breakage of corals at Low Isles during a cyclone in 1934 was described by Moorhouse (1936), and the 1950 cyclone evidently had similar effects.

However, various extreme conditions such as excessive rainfall and flooding have been reported as causing the death of corals in other regions. The cyclone in 1918 which struck central Queensland afforded a spectacular example of the effect of fresh water on coral populations (Hedley 1925; Rainford 1925), and unusually heavy rainfall accompanying a cyclone in 1951 caused destruction of coral in rock pools at Coral Point, near Sarina (Endean, Kenny, and Stephenson 1956).

The effects of flooding at Low Isles have been reported by Fairbridge and Teichert (1947, 1948). During January and February 1945, mud-charged waters from the flooded Daintree River extended to Low Isles, where they made the water "completely turbid". Live frogs, certainly of mainland origin, were cast up. Sediment was considered responsible for coral deaths and on the seaward slopes "much of the coral was dead and coated in a 'fur' of fine brown terrigenous sediment". This report is important, in view of the widely held opinion that floods have become increasingly severe in north Queensland owing to land clearance. If so, a new element—human interference—has entered the ecological complex, and coral growth may never attain its previous luxuriance.

However, analysis of data on rainfall and flooding in the area reveals that January and February 1945 were not especially rainy, nor were the floods in these months particularly severe. Similar floods resulting from the run-off from similarly cleared areas probably occurred on nine occasions following the 1934 cyclone, and during this period Fairbridge and Teichert reported a noticeable increase in coral growth. In the 5 years preceding the 1928–9 expedition, 10 floods were recorded but the coral growth was still luxuriant. Jamieson (personal communication) reports that during his 4½ years at Low Isles floods were frequent but damage to corals was negligible.

It seems likely therefore that the Low Isles corals are tolerably resistant to the combined effects of fresh water and mud which accompany flooding. This would be in agreement with the experimental work of Marshall and Orr (1931) at Low Isles, and with Moorhouse's (1936) opinion that mud removed from the mangrove swamp during the 1934 cyclone had negligible effects on the island's coral fauna. Additional observations in Queensland confirm that the coastal species of corals are resistant to muddy waters (Endean, Kenny, and Stephenson 1956; Endean, Stephenson, and Kenny 1956).

In discussing the effects of the 1950 cyclone on the Low Isles coral, and subsequent coral recolonization, the corals of the seaward slopes (including the anchorage) are separated from those of the moats.

(i) *Seaward Slopes.*—The south-western area was reported as escaping the effects of the 1950 cyclone, and many of the species which occurred there in 1954 (Table 22) were probably survivors of the original population. This probably

accounted for the dense growths of branching corals such as *Montipora divaricata* and *Acropora pulchra* in this area.

Apart from the south-western localities, the sparse and restricted coral populations of other areas (Tables 19–21) suggested that they had been affected severely by the 1950 cyclone. The most obvious surviving species were massive forms whose size implied a considerable age, and whose lack of dead areas implied almost complete survival. The important species were *Porites lutea* and *Goniastrea* spp., with the addition of *Symphyllia* on the north of the island.

Certain massive species possessed large dead and small living areas, and apparently regrowth had begun. These species, only of minor importance in 1954, included *Lobophyllia corymbosa* and *Pavona decussata*.

Other species are in a more uncertain category. Their compact structure suggests the possibility of resistance to the cyclone but their small size suggests that they may be post-cyclonic colonizers. Examples are *Leptastrea purpurea*, *Platygyra*, *Leptoria*, and the various species of *Favia*. Information on growth rates of corals at Low Isles is necessary for final categorization.

The remaining (fragile) species were probably completely or almost completely destroyed by the 1950 cyclone, and presumably have either regrown from stumps or have resettled. This category includes the various species of *Acropora* and *Montipora*, together with *Pocillopora damicornis* and *Stylophora*.

Further subdivision of the fragile species into rapid and slow recolonizers seems possible. The former are here considered to be species which have become medium-sized colonies. The most important were *Montipora divaricata*, *Acropora pulchra*, and *A. hebes* (Table 21), followed by *A. squamosa* (Tables 19, 20) and some of the lamellate *Montipora* spp. (Table 21).

Millepora tenera (Table 20) was an interesting case. At one site only, the fragile masses were a foot high and covered about a square yard. Whether this had regrown from stumps or had recolonized the area, an extraordinarily rapid growth rate must be postulated. Finck (1904) has commented on the enormous rapidity of growth of *M. alcicornis*.

If it is assumed that most of the small specimens are recolonizers rather than survivors, the different environments can be compared with respect to recolonization. On this basis, three interacting factors appear important: exposure to wave action, level on the beach, and presence or absence of "trickle".

The effect of exposure to wave action is clearly shown by comparing the variety of smaller species at L.W.S.: (1) in the most exposed situation (Table 20, column 5), (2) moderately exposed (Table 20, column 1), and (3) sheltered (Table 19, column 3). The respective numbers of species are 0, 17, and 13. Evidently recolonization had been most pronounced in moderately exposed situations. The deleterious effect of exposure was probably due to stirring up of sand.

Lower down the beach, recolonization in moderately exposed situations was much less than in sheltered ones. For situations 2 ft below L.W.S., compare Table 20, column 2 (two possible recolonizers) with Table 19, column 4 (23 probable recolonizers).

Trickle from the moats had an important effect (cf. Table 20, columns 3–5; and Table 21). At L.W.N. about 11 recolonizing species occur in trickle areas, as against one in the roughly comparable area without trickle. At M.L.W. the comparable figures are 19 and 12, and at L.W.S. 5 and 1. It should be noted that in this case drainage was from a mangrove-dominated area, and this might have had a deleterious effect. If "purer" water from the moat system could increase colonization, the coral abundance on the south-western side might be due more to recolonization and less to survival than has been postulated above.

(ii) *The Moats.*—Previously extensive *Acropora* beds were either absent or reduced to small areas. In the *Porites* pond patches of dead *Acropora* still *in situ* suggested that death had resulted from causes other than wave action, but in other moats the staghorns had evidently been reduced to rubble. Several species of great faunistic interest had disappeared (e.g. *Merulina*) or had become less common (e.g. *Heliopora*). Over most of the moats the dominant forms were such massive species as *Porites lutea*, *Goniastrea pectinata*, and *Platygyra lamellina*, and their abundance appeared unchanged since 1928–9. As on the seaward slopes, these appear to be the cyclone-resistant forms.

Several fragile species were common and widespread and had probably grown since 1950, especially *Montipora divaricata* and *Pocillopora damicornis*. *M. divaricata* was concentrated in shallow areas where water drained into and from the main moats. In the madrepore moat, small but apparently thriving patches of *Acropora* (*A. pulchra* and *A. hebes*) had become re-established.

The most important effect of the cyclone on the moat system was probably the encroachment of shingle upon the peripheral parts. In August 1954, shingle was still falling into the moats. Several large *Porites* colonies were being inundated and some were tilted by the weight of shingle.

Moorhouse (1936) noted that the drainage gaps in the moats were lowered during the 1934 cyclone, and the tops of corals killed. Comparable effects due to the 1950 cyclone were not detected in 1954, but may have been obliterated in the interim.

The apparent relationship between survival and massive structure in corals, both on the seaward slopes and in the moats, supports the suggestion that the mechanical effects of the swell accompanying the cyclone in 1950 were important. It seems probable that rainfall associated with the cyclone caused little damage to corals; firstly, because no excessive falls accompanied the cyclone; secondly, because damage was *least* in those areas which should have been most affected by rain, namely, the moats and the trickle areas leading from them.

The effect of silt associated with the 1950 cyclone would presumably be to destroy corals *in situ*, apart from those detached by the waves. Dead masses of *Acropora* were found in 1954 on the north-east part of the island and it is possible that the death of these corals was due to accumulations of silt. It is difficult to evaluate the relative effects of the muddy and sandy fractions of the silt, but the negligible effect of floods suggests that sand may have been the more important. Dead massive forms which remained *in situ* on the north of the island (Wishart's

Reef and Luana Reef) were considered by Dr. Dorothy Hill, who accompanied the 1954 expedition, to have a characteristically sand-blasted appearance.

There is the possibility that destruction of coral may have continued after the cyclone had passed. Moderate and possibly local destruction of *Acropora* would produce coral rubble whose subsequent movements could damage a much larger area, and would probably hamper recolonization by corals of areas already devastated. Further degradation into grit would assist this process, particularly in a bared area where this grit could be agitated by waves. In 1954 much of the lower seaward slopes of the eastern side of the island was characterized by a substratum of grit and rubble, and the grit was in fact kept in continual motion during moderate seas at low water. The delayed effects of the cyclone in the form of grit are believed responsible for the paucity of corals at about 2 ft below L.W.S. on the east and south-east sides where it would be expected that the corals would be densest. It is not impossible that a really severe cyclone would clear the area more completely of broken coral, and have less prolonged effects.

Another factor which might account, partially, for the slow rate of recolonization by corals in the north and north-west of the island is the competition of soft corals, which dominate most of the available habitats. The original report of the 1950 damage suggested that soft corals were unaffected, and since then they have probably spread to areas previously dominated by Madreporaria, particularly in the anchorage. Presumably the soft corals are important competitors of hard corals, and will decrease as, and if, hard corals become dominant.

It is evident that a prolonged period will elapse before there is a return to the flourishing conditions of 1928–9. Probably conditions in 1928–9 represented complete recovery from a severe cyclone in 1911, and by 1945 there was considerable recovery from the cyclone in 1934. It remains to be seen whether in the future recovery will be at an equal rate, or whether increased silting stemming from human activity will delay the process.

Data from other areas show widely differing recolonization rates. Rainford (1925), reporting on the effects of a flood in 1918 on corals in the Whitsunday Group, noted widespread destruction with only slight recovery 6 years later. *Acropora*, *Pocillopora*, and *Porites* were evidently playing the main roles in the process of recolonization. In the case of the most advanced recolonization (Hayman I.) he estimated that at least 10 more years would be required for complete recovery, and in other cases doubted if recovery would ever occur. One of the worst-devastated areas was Stone I. near Bowen, much photographed by Saville-Kent (1893). In 1953, after 35 years, Professor F. W. Whitehouse (personal communication) reported negligible recolonization on this island.

(*b*) *Changes in the Specific Composition of the Fauna since 1928–9*

The overall changes undergone by the Low Isles fauna during the 25 years preceding 1954 are difficult to assess. The habitats investigated by the 1954 expedition were in many cases not identical with those examined by the 1928–9 expedition, and the extent to which those examined by the 1928–9 expedition have changed is uncertain. Moreover, the varied habitats were not all examined in a comparable

fashion. Thus the manner in which major habitats were subdivided by the two expeditions often differs, and it is probable that the 1928–9 expedition examined some habitats more intensively than the 1954 expedition did and vice versa. Changes in the synonymy of various species have added further complications.

Some species recorded in 1928–9 were not observed in 1954. For example, *Arachnanthus*, *Phymanthus*, *Macrophthalamus telescopicus*, and *Cardium oxygonum* were not found although these species were apparently common in 1928–9 on the sand flat. *Cyphastrea* was not found on *Rhizophora* roots in 1954 although it was in 1928–9. Some species were found in 1954 (e.g. *Pagurus deformis*, *Clibanarius virescens*, *Thalamita admete*, *Portunus granulatus*, *Calappa* spp., and *Penaeus* sp.) but not in 1928–9.

However, it would appear that changes in the faunistic composition of corals (Stephenson and Wells 1956), and echinoderms (Endean 1956), have been slight, and the results of the present survey do not reveal significant changes in the composition of other faunistic groups.

(c) *Ecology of the Stony Corals*

One of the outstanding difficulties in coral ecology is the occurrence of an extraordinary variety of species in a given habitat. The present survey indicates that from this complexity two main ecological types can be recognized at Low Isles, viz. the massive, robust forms which are cyclone-resistant, and the branching or lamellate fragile forms which are destroyed in cyclones. Massive species include: *Porites lutea*, *Goniastrea retiformis*, *G. pectinata*, *Lobophyllia corymbosa*, *Symphyllia*, and possibly *Leptastrea purpurea* and some species of *Favia* and *Favites*. Fragile forms include the numerous species of *Acropora* and *Montipora* and also *Pocillopora damicornis*. When the coral growth as a whole is flourishing, the fragile species predominate, and it would seem that they recolonize more readily and grow more rapidly than the massive forms.

The estimates of Wood-Jones (1912) of growth rates of coral at Cocos Keeling I. support this contention. He found that the average growth at the tips of branching forms was 3·7 in. per year while the height of massive hemispherical forms increased at only 0·6 in. per year. Guppy (1889) found that in the lagoon at Cocos Keeling I. branching *Montipora* grew upwards at not less than 5 in. per year, branching *Acropora* at 4–5 in. per year, but massive *Porites* only at ½ in. per year. Vaughan and Wells (1943) have summarized more recent work and have shown that the porous species of corals, especially the branching ones, grow much faster than others.

Although most of the Low Isles corals must have a tolerable resistance to both fresh water and suspended mud, *Leptastrea purpurea* is probably one of the most resistant. It occurred in muddy mangrove regions at Low Isles and is common in intertidal rock pools on the Queensland coast.

Several species of corals are (and were in 1928–9) rare or absent at Low Isles although common on the outer reefs, for example, at Yonge Reef (Stephenson *et al.* 1931) and at Heron I. (Salter 1954; Stephenson and Wells 1956). These include *Acropora brueggmanni*, *A. digitifera*, *A. cuneata*, and species of *Plesiastrea*, *Stylophora*, and *Tubipora*. These species may be adversely affected by floods and sediment.

Alternatively they may require greater wave action than is available at Low Isles, and it is noteworthy that the most abundant corals at Low Isles (*Montipora divaricata* and *Acropora pulchra*) seem to be species generally found in sheltered habitats. Thus at Cocos Keeling I. (Guppy 1889; Wood-Jones 1912) both species are very common in the shelter of the lagoon. At Heron I., which is too far south for *M. divaricata*, *A. pulchra* is very common in the deeper pools behind the reef crest in the lee of the coral cay, and about 10 ft below and beyond the reef crest, all these situations being sheltered.

The vigorous coral colonies growing amongst the mangroves, and in many cases attached to *Rhizophora* stilt roots, were commented on by Stephenson *et al.* (1931) and in Section VI(*a*) of this paper. The richest growth in 1954 was in the main eastern drainage channel from the mangrove swamp. There is no field evidence supporting the statement of Fairbridge and Teichert (1948, p. 82) that: "It seems likely that the concentration of carbonic acid and other deterrents from the adjacent mangroves is prohibitive for coral growth".

Of interest was the close association of mushroom corals (*Fungia*, *Polyphyllia*, and *Parahalomitra*) with soft corals.

(*d*) *Cyclone Debris*

During or soon after cyclones, coral fragments are deposited in quantity at higher levels. The worst cyclones produce boulders (Hedley 1906; Hedley and Taylor 1908; Wood-Jones 1912; Mayer 1918). At Low Isles boulders are concentrated on the north-west, where they form a boulder zone. A similar leeward boulder accumulation occurs on a New Caledonian island (Catala 1950), but windward concentrations have been recorded (Hedley and Taylor 1908).

Since 1928–9 no new boulders have been deposited at Low Isles. As noted in Section VII(*b*), the boulders at Low Isles have distinct "waistlines" from which coral rock had obviously been removed. By a comparison of waistlines in 1928–9 (Stephenson *et al.* 1931, Plate V, Fig. 4) with those in 1954, it is estimated that a slightly greater reduction in diameter has occurred since 1928 than before. A reduction of approximately 1 in. annually seems likely—roughly half the rate estimated by Hedley and Taylor (1908). This would indicate that the boulders were deposited about 20 years before the 1928–9 photographs were taken. Reference to records of cyclones kept since 1885 show that cyclones of exceptional severity struck the Low Isles area in 1905 and 1911. Probably one of these was responsible for the present boulder zone.

The mechanism of removal of coral rock from boulders and beach rock has been the subject of much speculation. Solution of rock by sea-water has been claimed to be responsible (Kuenen 1933, 1950; Umbgrove 1939; Emery 1946); but there is little evidence that the pH of sea-water is ever low enough to allow this solution (Newell 1954). Various organisms ranging from blue-green algae (Newell 1954) to gastropods (Doty 1954; Newell 1954; Newhouse 1954) and parrot fish (Wood-Jones 1912) have been suggested as being responsible for coral rock removal.

At Low Isles parrot fish do not appear to be abundant, and the main agent of destruction appears to be the chiton *Acanthozostera*. The waistline of the boulders

is at the level of the greatest abundance of the chitons, and numerous abrasion marks caused by their radulae were noted.

The commonest debris at Low Isles is coral shingle derived from erect branching staghorns. In moderate weather the shingle accumulates progressively about half way down the intertidal seaward slopes (Spender 1930; Moorhouse 1936); but during cyclones this accumulated shingle plus newly broken fragments is transported up the beach to form, or add to, the shingle ridges. The movements of this shingle and of grit derived from it has important effects on the fauna (see Section IX(*a*)(i)) and in many areas probably hampers recolonization by corals.

On the eastern side of the island the seaward slope bears landward-dipping ridges of shingle partially consolidated into rock. Steers (1937) considered that they were the remains of ancient shingle ramparts whose present erosion is due to a lowered sea-level. The present authors suggest that they are due to cyclone removal of calm-water aggregations of shingle. The movement of shingle, and differing degrees of consolidation of the exposed surfaces, together with differing amounts of organic cementing, result in a complicated mosaic of habitats on the eastern shores. At and below M.S.L. two main types of habitat are worthy of special attention: the hard "honeycomb" rock and the smooth rock surfaces. The honeycomb rock is dominated by the ring cowrie (*Monetaria annulus*) and the smooth rock by a mussel (*Modiolus*). The distinction between the two faunas is so obvious that they may well serve as indications in future surveys.

(*e*) *The Permanence of the Moat System*

The effect of cyclones upon the moats seems to be threefold: (i) destruction of corals and clams; (ii) inward movement of the shingle ramparts forming their outer borders; (iii) alteration of the heights of the ramparts and the level of water in the moats.

The destruction of coral in the moats has been described (Section IX(*a*)(ii)) and Moorhouse (1936) has commented on the destruction of clams. Probably the abundant detritus in the moats originated in this way. Sand fills the interstices in the broken corals, and fills the valves of the dead clams. The spaces between pieces of these materials also become filled with sand and with the skeletons of the abundant foraminiferan, *Marginopora*, thereby protecting the detritus from boring and abrading species. However, prolonged studies are required if the importance of detritus in the moats in raising the level of the floor of the moats is to be evaluated.

Moorhouse (1936) noted that during the 1934 cyclone the shingle ramparts moved inwards and obliterated the other parts of the moats. There was abundant evidence that the 1950 cyclone had a similar effect. If this happens in every case of cyclonic damage there is a possibility that the moats may eventually be obliterated as a result. Between 1928 and 1945 one moat, the north-eastern, was so obliterated, and no trace remained in 1954.

In addition, in shallow water the growth of massive hemispherical species which later become micro-atolls must progressively reduce the volume of water; Plate 8,

Figure 1, indicates the importance of this process. Stephenson *et al.* (1931) suggested that the honeycomb rock in the mangrove park arose in this way, and the present authors regard it as probable. Finck (1904) has also noted at Funa-Futi that large masses of *Porites* unite with their neighbours to form continuous level surfaces.

Water in the moats is held back by the shingle ramparts and, at low water, drains through gaps down the outer slopes. The depth of the water in the moats will depend on the height of the gaps above sea-level. Moorhouse (1936) noted that the heights of the gaps were lowered by the 1934 cyclone, and that this resulted in lowering of moat level, and killing of the tops of moat corals. There were no indications in 1954 that the 1950 cyclone had had a similar effect. Concentrations of rubble may well fill in some gaps and assist in the development of others. Since 1928–9 the old gap D has disappeared, and by 1945 a new eastern gap had developed (Fairbridge and Teichert 1947, 1948).

Growth of living coral and lithothamnion in the gaps may have a minor effect upon the amount of water in the moats. In 1954 the rapid-growing *Montipora divaricata* and lithothamnion were common in these habitats. Their effects are: firstly, to make the shingle more impervious to water and to canalize the flow; secondly, to impede this flow. After a period of climatic stability a slight raising of water level may be expected.

To maintain the floor level in the moats, material should be removed at a rate equivalent to its accumulation. The first necessity is the reduction of shingle to smaller particles which can be transported by water currents. In this respect the activities of most of the boring organisms at Low Isles are negligible, either because they prefer fragments larger than shingle or because they occur between high and low water marks (Otter 1937). However, in water more than 6 in. deep *Diadema* is so abundant as to suggest an important role.

In debris consisting of masses larger than shingle, the clam *Tridacna crocea* and the echinoid *Echinometra* are frequently found, and these organisms probably assist in the degradation of these masses to finer particles. The role of *Echinometra* in abrading away coral debris has been observed at other localities (Umbgrove 1939; Bonner 1952; Doty and Morrison 1954; Morrison 1954).

Once the accumulations of detritus in the moats have been reduced to sand or finer particles, current transport will probably remove these materials from the moats. As noted by Stephenson *et al.* (1931) considerable currents are present within the moat system. Part of the transported sand settles on the sand flat, part accumulates at the sand cay, and part drifts seaward from the anchorage to form a leeward tail (Fairbridge and Teichert 1947, 1948). The centre of the flat has a distinct channel through which sediment evidently passes to the anchorage. The scour in this channel is considerable, and the only sign of its filling up is the extremely slow marginal growth of corals, especially *Porites lutea*.

There is no certainty that the processes of accumulation within the moats at Low Isles are in equilibrium with the processes of removal, and it is conceivable that the floor level is rising progressively. Certainly the reef flat at Low Isles is at "an unusually high level" (Stephenson *et al.* 1931, p. 94), viz. 3 ft above datum.

There is, however, no necessity to postulate a lowering of sea-level to account for this, as Stephenson *et al.* have suggested.

If the flat is gradually rising, a stage will be reached, in the absence of complications due to mangroves, when coral growth in the moats effectively ceases, and practically all of the flat would then be an elevated sandy expanse. This state may have been attained at Piper I. (Wells, personal communication). Future additions would then be peripheral rather than vertical.

On the other hand Mayer (1924) and Umbgrove (1940) have pointed out that in large structures current transport may remove more material than accumulates. This would explain some of the conditions at Heron I. Here, currents adjacent to the cay attain a speed of 5 knots, cyclonic debris is restricted to a peripheral fringe, and the cay, according to residents of 25 years' experience, is slowly declining in size. Data on rates of deposition and removal of sand over a prolonged period at key points at Low Isles are required.

(*f*) *Mangrove-dominated Habitats*

(i) *Spread of Mangroves.*—Because of the rapid rate of spreading of *Rhizophora* between 1928 and 1945, and again from 1945 to 1954, it would appear that mangroves are a recent introduction to the island. Since 1945, *Rhizophora* seedlings have become widespread in the *Porites* pond, in the southern moats, and south of the cay, and this gives the impression of a rapidly spreading population. It is possible that most of these seedlings will die, as have the thriving fringe of seedlings on the north of the *Porites* pond noted by Fairbridge and Teichert (1947, 1948). However, a slow spreading seems inevitable, and possibly the south of the cay may soon be colonized, as has happened at Three Isles (Stephenson *et al.* 1931). Eventually the entire flat may be converted into a mangrove swamp. Steers (1937) believed that fully wooded islands to the north of Low Isles are a later phase in an evolutionary process leading in this direction.

(ii) *Mangrove Mud.*—A number of authors have ascribed the accumulation of mud in mangrove swamps to the destruction of coral rock by the mangroves. In addition to this possible source, the mud around mangroves at Low Isles may be derived from coastal floodings, mangrove tissues, and degradation of corals by organisms outside the swamp. Fairbridge and Teichert (1947, 1948) suggest that the decomposition of coral fragments by mangroves will result in a loss of material from the structure as a whole. However, if mud accumulates in the mangrove swamp, the area will build up rapidly, and it is perhaps significant that in 1928–9 the eastern part of the flat which contains the mangroves was about 1–1½ ft higher than the western part.

(iii) *Mangroves and Shingle.*—On the eastern side of the island the mud of the mangrove swamp gave way to a succession of shingle ramparts with the outermost and most recent beyond the mangroves proper. Outside the last rampart a few clumps of stunted *Avicennia* grew from semiconsolidated shingle.

It seems likely, as Steers (1929) has suggested, that the ramparts have preceded the mangroves at Low Isles. Probably mangroves assist in the accumulation

of shingle. Certainly shingle ramparts were wider and higher in the mangrove area than elsewhere. Mangroves (mainly *Bruguiera*) seem to establish themselves progressively, and act as shingle traps. Because the outer ramparts give an impression of extending progressively further outwards, and since shingle from recent cyclones has been deposited high up in this area, it is suggested that at Low Isles the mangrove shingle habitat is one with an inherent tendency to rapid growth, and also that it is of fairly recent origin. Stephenson *et al.* (1931) suggest that the asymmetrical shape of Low Isles may be due to the fusion of two adjacent reefs. It seems equally possible that the asymmetry is due to a more rapid upbuilding of the easterly portion, related to the rapid spread of the mangrove shingle areas.

(*g*) *The General Ecology and Biogeography of the Commoner Animals*

The general ecology and biogeography of corals (Wells 1955; Stephenson and Wells 1956), and of echinoderms (Endean 1956, 1957) at Low Isles have already been discussed, and these groups are omitted from subsequent discussion.

(i) *The Fauna of the Beach Rock, Boulders, and Mangrove Stems.*—The fauna of the beach rock may be taken as a basis for discussion of the fauna of similar habitats (e.g. boulders and mangrove stems) at Low Isles and elsewhere. Four zones were distinguishable on this rock: "bare", oyster, algal, and *Chama* zones (Section V(*b*)). The bare zone is effectively a littorinid zone, comparable with those in other parts of the world (Stephenson and Stephenson 1949). It showed a closer resemblance to conditions on the north Queensland mainlaind, where there was an upper *Nodilittorina* subzone and a lower *Melaraphe* subzone (Endean, Kenny, and Stephenson 1956), than to conditions at Three Isles, where the order was *M. coccinea*, *Tectarius malaccana* (= *Nodilittorina*), and *M. undulata* (Stephenson *et al.* 1931). This sandwiching of *Nodilittorina* between two *Melaraphe* populations is apparently intermediate between conditions on the north Queensland mainland and those of the mid Pacific islands, where *Melaraphe coccinea* becomes the uppermost species, followed by "*Tectarius*" (Doty and Morrison 1954; Newell 1954). *M. undulata* and *Nodilittorina* are common at Singapore (Purchon and Enoch 1954).

The boulders did not extend high enough to accommodate a littorinid population. A littorinid, *Melaraphe scabra*, is present on mangrove stems. It extends southwards to beyond Sydney (Dakin, Bennett, and Pope 1952) and occurs in east Africa (Kalk 1954). On the Queensland coast it is not rigidly restricted to mangrove stems. Specimens have been noted on shingle and rocks near mangrove areas.

The lower half of the bare zone on the beach rock is populated by *Planaxis*, *Nerita polita*, and *N. plicata*. These are widespread in Queensland coastal waters, where they occur typically on sheltered stony beaches, but *N. plicata* is never very common. At Heron I. this species is common under slabs of beach rock, and in mid Pacific islands it is abundant (Doty and Morrison 1954; Newell 1954).

In more exposed situations in north Queensland the *Planaxis-Nerita* association is replaced by *Chthamalus malayensis* (Endean, Kenny, and Stephenson 1956).

The oyster zone is only moderately developed on the beach rock, and the population is slightly denser at equivalent levels (roughly H.W.N. to L.W.N.) on

Rhizophora stems, and much denser in the boulder zone. An oyster occurs in an identical habitat in eastern New Guinea (Umbgrove 1940). The present species, *Crassostrea amasa*, is the dominant animal on regions of the north Queensland coast where there is appreciable wave action (Endean, Stephenson, and Kenny 1956). Variations in the amount of wave action probably explain most of the local variations in oyster populations at Low Isles. Observations here and elsewhere in Queensland suggest that whenever oysters are particularly dense, the remaining fauna at this level is sparsely represented, and in particular there may be an inverse relationship between the relative densities of oysters and *Acanthozostera*. Thus at Heron I., the beach rock is almost devoid of oysters, and *Acanthozostera* is a dominant. On the continental islands oysters form a wide and dense band, and here *Acanthozostera* is, at most, "common" (Endean, Stephenson, and Kenny 1956). The beach rock and boulder zone at Low Isles are between these extremes, and on the boulders the two populations are distinctly stratified, with an oyster zone above and an *Acanthozostera* zone below.

Oysters are common on the peripheral mangroves but the more central areas of the mangrove region are without oysters. It is noteworthy that a second species of oyster (*Crassostrea echinata*) occurs in the more muddy mangrove areas.

The associates of the oysters are of interest. They include *Morula marginalba*, common in New South Wales and southern Queensland. As in many other groups, an increased specific variety of predatory whelks occurred at Low Isles, as compared with further south, and four species of *Morula* were collected. Other associates, including *Perna* and an unidentified anemone, occupy crevices between the oysters.

An algal zone, occurring at approximately L.W.N. on the beach rock, is not a usual phenomenon either at Low Isles or on the mainland coast. However, a similar zone occurs on the beach rock at Heron I. On the boulders at Low Isles at equivalent levels there is an *Acanthozostera* zone with a few barnacles (*Tetraclita vitiata* and *T. coerulescens*), while on the mainland coast there is usually a distinct *T. squamosa* zone.

The *Chama* zone on the beach rock is typical of flat or gradually sloping coral rocks, and is equally developed on "micro-atolls" and the honeycomb rock of the reef flat. By contrast, *Chama* is poorly represented on the near-vertical boulder faces. A *Chama* zone was noted by Hedley and Taylor (1908) at Hope I. reef. Wells (1951) has also recorded a *Chama* zone at Arno Atoll in the Marshall Islands. At Heron I. the equivalent level on the reef edge is occupied by zoanthids, and apparently the same applies at Cocos Keeling I. (Wood-Jones 1912). This zoanthid zone is represented at Low Isles only by occasional patches of *Palythoa* in the boulder zone; and on the Queensland mainland generally, zoanthids are sporadic in their occurrence.

Only one of the rocky habitats at Low Isles extends down to L.W.S. and below, viz., the boulders. Here the dominant form is the boring clam *Tridacna crocea*, which is definitely restricted to a calcareous substrate.

(ii) *The Fauna of the Sand Flat.*—The surface fauna of the sand flat at Low Isles, as at Heron I., is characterized by *Strombus gibberulus* and by a variety of

naticids and nassarids. On sandy flats on the mainland coast a different fauna occurs. Here soldier crabs (*Mictyris*) are abundant, there is a different common portunid (*Portunus pelagicus*), a different *Phyllodoce*, and different naticids (*Uber strangei* and *U. conicum*).

The subsurface fauna of the sand flat at Low Isles has resemblances to that of Funa-Futi (Hedley 1899) in an equivalent abundance of *Circe pectinata* and *Atactodea*, and especially to that of the Gilbert Is. (Bonner 1952; Cloud 1952) where *Ptychodera*, *Circe pectinata*, and *Atactodea* are very common.

The steeply sloping sandbanks near the cay have two distinct zones, an upper *Ocypode* and a lower *Davila* zone. The former is a widespread and well-known ecological entity. In Queensland generally *Ocypode ceratophthalama* is dominant as it is in Hawaii (Edmondson 1946) and Christmas I. (Andrews 1900). In southern New South Wales the less common northern species *O. cordimana* becomes dominant (Dakin, Bennett, and Pope 1952). Throughout the Indo-Pacific region a variety of ocypodes is found, and although not common on the west coast of North America the genus is important on the east coast. It occurs in the Mediterranean, and also on the west coast of Africa.

The zone of amphidesmid bivalves (*Davila*) again represents a widespread ecological entity, but one upon which attention has not previously been focused. Another genus (*Atactodea*) is abundant at Funa-Futi (Hedley 1899), occurs in close-packed patches at mid-tide level on the sandy beaches of the Gilbert Is. (Cloud 1952), forms a zone at about L.W.N. on the sloping intertidal sand of the cay at Heron I., and occurs in patches on sloping gritty sand in Moreton Bay. Amphidesmids are common in South Australia (Cotton and Godfrey 1938; Johnston and Mawson 1946) and are dominants in New Zealand (Rapson 1952, 1954).

(iii) *The Fauna of the Moats.*—This is diverse, and only the more obvious constituents will be mentioned. Several species do not extend southwards to the Capricorn Group, e.g. the clams *Tridacna crocea*, *T. derasa*, and *Hippopus hippopus*. Other species extend to Heron I. but are less common there, e.g. *Lambis lambis*, *Monetaria annulus*, and *Trochus niloticus*. Some extend to Moreton Bay or even further south, e.g. *Atergatis floridus*, *Thalamita stimpsoni*, *Aplysia angasi*, *Amphiperas ovum*, *Monetaria annulus*, *Arabica arabica* (and several other cowries), *Strombus luhuanus*, and *Isognomon isognomon*.

Outside Australia, the Low Isles moat fauna has obvious resemblances to that in equivalent habitats at Cocos Keeling I. (Wood-Jones 1912), at Funa-Futi (Hedley 1899), at New Caledonia (Catala 1950), and in the Gilbert Is. (Bonner 1952). Several of the species are also common forms on rocky shores at Singapore, for example *Trochus niloticus*, *Lambis lambis*, and *Isognomon isognomon* (Purchon and Enoch 1954).

(iv) *Fauna of the Mud and Shingle in the Mangrove Area.*—The mangrove mud carries a distinctive fauna which characterizes large areas of the tropical Queensland coast. The dominant surface species are *Terebralia* and *Telescopium* which extend southwards to Gladstone. South of Gladstone the equivalent habitat is dominated by *Pyrazus australis* and *P. ebeninus*. These species, however, extend beyond the mangroves to the muddy *Zostera* flats.

Other species associated with mangrove mud include *Periophthalmus* and various Crustacea, especially *Sesarma*. Again these extend southwards to Gladstone but the majority do not occur in Moreton Bay.

In the case of animals on rocky shores, a biogeographical boundary occurs on the Queensland coast at about 25°S. (Endean, Kenny, and Stephenson 1956), and it is of interest to note indications of a similar faunistic discontinuity at roughly the same latitude in a quite different habitat.

The fauna of the muddy shingle areas of the mangrove swamp includes several species which occur equally abundantly on and under stones, and in shingle away from the mangroves. Many extend southwards to Moreton Bay (e.g. *Nerita albicilla*, *N. lineata*, and *Planaxis*), and some extend westwards to Mozambique in east Africa (Kalk 1954) and eastwards into the Pacific (e.g. *N. albicilla* and *Planaxis*).

The shingle-dwelling gastropods *Quoyia*, *Bembicium*, and *Onchidium* were concentrated amongst the shingle under *Bruguiera* bushes. Provision of shade seems the key to this association.

Of interest is the abundance of fish between the mangrove prop roots. Some of the species of fish found in this habitat are usually found associated with coral.

(v) *The Fauna of the Seaward Slopes*.—Right round the island wherever loose shingle occurred, algal populations formed zones which compare collectively with Umbgrove's "*Rhodophycaea* facies" in the Bay of Batavia (Umbgrove 1928). A noteworthy difference is that Umbgrove's dominant genus was *Amphiroa*. This genus is also dominant at Raroia, Tuamotu Is. (Doty and Morrison 1954) but was unimportant in the present case, where *Gelidium* was conspicuous.

Lithothamnion is inconspicuous around most of the periphery of the island. Only on the exposed eastern side, and below M.S.L., is it at all obvious. Here it probably plays an important role in cementing loose coral fragments. Indeed the existence of masses of loose shingle at Low Isles may be attributed partially to the paucity of coralline algae, which, at more exposed localities, cement together coral debris.

As noted in Section VIII(*b*) soft corals were abundant in the anchorage and on the northern side of the island generally. Soft corals dominate the reef flat in the lee of Murray I. (Mayer 1918), and are widely distributed throughout north Queensland (Saville-Kent 1893).

The dominance of honeycomb rock areas on the eastern side of the island by a cowrie (*Monetaria annulus*) has been commented on in Section VII(*a*). *M. annulus* is very common amongst rubble on the reef crest at Heron I. It is the commonest cowrie near New Caledonia (Catala 1950) and extends at least as far westward as Cocos Keeling I. (Wood-Jones 1912). In the Gilbert Is. (Bonner 1952) and the Tuamotu Is. (Morrison 1954) the closely allied money cowrie (*Monetaria moneta*) is reported as having an almost equivalent ecological status.

On areas adjacent to the honeycomb rock, smooth rock is found, and here a mussel, *Modiolus*, is dominant. Mussel zones are a widespread and well-known ecological entity. In Australia they have been reported from coastal rock platforms in Victoria (Bennett and Pope 1953).

(vi) *The Fauna of the Under-Stone Habitat.*—This fauna is difficult to analyse, because it is uncertain what proportion of the fauna is permanently located in the habitat, and what proportion merely retreats there during the daytime at low water, which is the only time when normal observations can be made. Some indications of this fraction are obtained by comparing the under-stone fauna with that of the surrounding substratum. Species characteristic of the surroundings are presumably merely sheltering under the stones. On this basis such species as *Strombus gibberulus*, *Uber* spp., and *Thalamita admete* are primarily sand and grit dwellers sheltering under adjacent stones, just as *Acanthozostera* is primarily a rock dweller.

Another distinct category is the fauna under embedded rocks. Many of the species are merely burrowers in the surrounding substratum (e.g. *Ptychodera*), and yet others are concentrated in this habitat, probably at the periphery of stones (e.g. *Eurythoë* and *Promantellum*).

It is difficult to separate the under-stone fauna from the fauna of open shingle.

(*h*) *Information Still Required*

The 1954 expedition was too short to examine all available habitats. Four in particular need further investigation:

(1) The seaward slopes more than 2 ft below L.W.S. As far as could be seen, this was a barren area with occasional living pillars of coral, mostly of *Porites*, but further investigations with use of a boat are required.

(2) The mosaic of habitats on partly consolidated shingle rock on the eastern side of the island.

(3) The sandy area to the north-east of the main mangrove area. Here burrowing forms, probably callianassid crustaceans, may limit the spread of mangroves.

(4) The fauna associated with living coral branches.

Further visits to Low Isles are also required to obtain information on the later stages of recovery from the 1950 cyclone, assuming that they will occur. To date there has been a detailed survey in 1928–9, a brief survey in 1945, and a brief but reasonably intensive survey in 1954. Another survey in the 1960's would be particularly valuable.

Quantitative work on many aspects touched on in the present discussion is also required; for example, on the rate of removal of limestone from the boulders in relation to the size of the *Acanthozostera* population, on the effect of *Diadema* on moat shingle, on the rate of growth of the mangrove shingle habitat, and on the rate of growth of some of the more important corals.

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EXLANATION OF PLATES 1–11

PLATE 1

Fig. 1.—Sand cay viewed from the east, showing sand beach and beach rock.

Fig. 2.—*Chama* zone on beach rock, with burrows of *Lithophaga dichroa* (XV).

PLATE 2

Fig. 1.—A typical collection of animals from under rocks.

Fig. 2.—*Rhizophora* in mangrove park with oyster zone at base. *Inset: Melaraphe scabra* on trunks (XXIX).

PLATE 3

Fig. 1.—*Ceriops* thicket with sand and grit substratum (XXXII).

Fig. 2.—*Rhizophora* stilt roots, so thick that clear water cannot be seen. Fish caught by hand near here (XXXVII) saved a temporary food shortage.

PLATE 4

Fig. 1.—Muddy mangrove area near Green Ant I. (XXXIX). The abundant mud-creeping gastropods and difficulty of the terrain will be noted.

Fig. 2.—Upper mangrove shingle habitats just within the mangrove forest (XXXVIII).

PLATE 5

Fig. 1.—Muddy mangrove shingle near Green Ant I. (XXXIX(2)).

Fig. 2.—Sand flat viewed from the south, with beginnings of rubble area inshore on extreme left, and beach sandbank behind.

PLATE 6

Fig 1.—From the *Thalamita* flat, looking towards the east.

Fig. 2.—Madrepore moat (XXVIII) in left middle distance and *Thalamita* (stony) flat in right middle distance. In the left foreground, note the steep shingle wall.

PLATE 7

Fig. 1.—West side of *Porites* pond (VII), showing *Porites* micro-atolls and *Tripneustes* spit immediately behind the pond.

Fig. 2.—Density of *Diadema* in the E. moat (XXXVII).

PLATE 8

Fig. 1.—Rounded corals in moat practically covering surface.

Fig. 2.—Semiconsolidated shingle and "crumbly" beach rock on eastern side of island.

PLATE 9

Fig. 1.—Clusters of *Planaxis* in loose brown shingle at H.W.N. on eastern side of the island (XXXI(1)).

Fig. 2.—Rough-surfaced, partly consolidated shingle on eastern side of the island at L.W.N., dominated by *Monetaria* (XXXIII).

PLATE 10

Fig. 1.—Mussel beds (*Modiolus*) on hard consolidated shingle at L.W.N. on eastern side of the island (XL).

Fig. 2.—Fauna of boulders on the boulder tract (XXIV). Note the oyster zone followed by the bare (*Acanthozostera*) zone, in which the boulder is perforated.

PLATE 11

Fig. 1.—Probably the densest coral growths on the island, in the trickle area, south-west side of the island at M.L.W. (XII). The commonest species were *Acropora pulchra*, *A. hebes*, and *Montipora divaricata*.

Fig. 2.—Corals at L.W.S. in the trickle area on south-west side of the island (XIII). The dominant species was *Acropora pulchra*.

MARINE FAUNA OF LOW ISLES

MARINE FAUNA OF LOW ISLES

MARINE FAUNA OF LOW ISLES

1

2

MARINE FAUNA OF LOW ISLES

MARINE FAUNA OF LOW ISLES

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MARINE FAUNA OF LOW ISLES

MARINE FAUNA OF LOW ISLES

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2

THE POPULATION OF A TROUT STREAM AND THE SURVIVAL OF RELEASED FISH

By A. G. Nicholls*

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Summary

The fish population of a river system was studied by electro-fishing in 25 places, after which 1000 marked yearling brown trout, *Salmo trutta* L., were released at each of 10 sites. In a re-examination 8 to 9 months after the release it was estimated that about 10 per cent. of these were surviving; the survival after 18 months was estimated to be below 5 per cent., and the survival to takable size, at about 3 years of age, at 2 per cent. At no site were the younger age groups of the natural population truly represented in either season, but the numbers of older fish in the second season were greater than those of the corresponding year classes in the preceding season, showing that the streams receive recruitment of younger fish from other sources. Some evidence is produced to show that "nursery" streams provide the source of recruitment. The average annual mortality for fish of 2 and 3 years of age is estimated at from 70 to 80 per cent. for the system. It is estimated that there were about 45,000 takable fish in this river system at the beginning of each season. It is shown that the mean lengths of trout decrease with increasing density of population, and that there is a curvilinear relationship between population density and total weight of all fish per acre. The standing crop of trout at different sites ranged from 1 to 182 lb/acre over the two seasons. The condition factor showed a decrease with increasing age of the fish, and the released fish had a lower factor than resident fish of the same age at all sites. In general there was a relationship between the depth of water and the length of the fish, sections over 14 in. deep having greater populations of larger fish. A study of the ability of each section of stream to carry fish, based on the lengths and condition factors of the fish, the number and weight of the population per acre, and the ability of each section to absorb additions to the population, shows that where populations were low, conditions were less favourable to the growth and survival of fish.

I. Introduction

In two earlier papers (Nicholls 1958*a*, 1958*b*) it was shown that on the basis of the rates of stocking various Tasmanian streams the contribution made to anglers' catches from such fish could not have exceeded certain proportions (varying from 2 to 10 per cent.) of the total catches made by anglers. In making these estimates it was assumed that the released fish suffered the same mortality rates as the wild fish, and it was not possible to relate the survivors to the existing population owing to lack of data on the latter. In the light of evidence which showed that in two streams where marked fish had been released no survivors were found 20 months later when the places of release were fished by the electric method, it was thought that the mortality rate of released fish might be higher than that suffered by wild fish, or that the released fish might have become dispersed beyond the area of

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release. The present paper gives the results of an attempt to follow the fate of released fish and to discover what relationship such fish bore to the natural population when the selected stream was stocked at a comparatively high rate.

The North Esk System was chosen for this experiment for several reasons: (i) it is a compact system which normally carries good fish; (ii) it has many tributaries suitable for the release of yearling fish; (iii) both these and the main streams are crossed by roads or are accessible from the road at numerous places, conditions essential for a survey with the heavy equipment required for electro-fishing; and (iv) in the opinion of anglers, as expressed in the 56th Annual Report of the Northern Tasmanian Fisheries Association (1954), both the North Esk and St. Patrick's Rivers required heavy restocking. It may be noted that during the 10 years up to 1951 this system had been stocked with brown trout, *Salmo trutta* L., at a rate equivalent to an average of 2500 yearlings annually, and that during the four subsequent years the average rate was 3600 annually. Because of the increased rate of stocking it is not possible to state that all or the majority of fish found in the streams during this study were naturally spawned fish, but it will be possible to discover the results of releasing marked fish into the existing population. A general account of the physiography of this area has been given earlier (Nicholls 1958*b*).

II. Methods

(*a*) *Method of Operation*

During December 1954 and January 1955 sections of the North Esk and St. Patrick's, and their tributaries, were fished at 25 places: 14 in the North Esk and 11 in the St. Patrick's (Fig. 1 and Appendix I). In June 1955, 1000 marked yearling brown trout were released at each of 10 sites, selected with a view to giving the small fish the best chances of survival. Fish released in the North Esk streams had their left pelvic (ventral) fins removed and those released in the St. Patrick's lost their right pelvic fins. When marking fish by this method it is important to ensure that the fin is removed as close to its base as possible, as tests have shown that unless this is done regeneration can occur sufficiently rapidly to make later recognition difficult. In this study, marked fish recaptured were usually easily recognized but in order to eliminate the risk of overlooking released fish, all those with asymmetry in the pelvic fins were regarded as having been marked.

It was intended to fish the same 25 sections again as near as possible to 12 months after the initial study, but the summer of 1955–56 was marked by a series of heavy falls of rain at intervals which made it difficult to keep to any set programme. It was not possible to make a start on this work until February 1956, and it was constantly interrupted so that it was not completed until March 21. Even then several of the sections in the main streams could not be worked owing to the increased depth and current and these had to be abandoned. One of the original, and six additional, sections were fished in December 1956.

At each site, which was closed by stop nets at both ends, the length of the stream was measured along its centre, and the width, and the depth at the centre, were measured at 18-ft intervals. From these measurements the approximate area

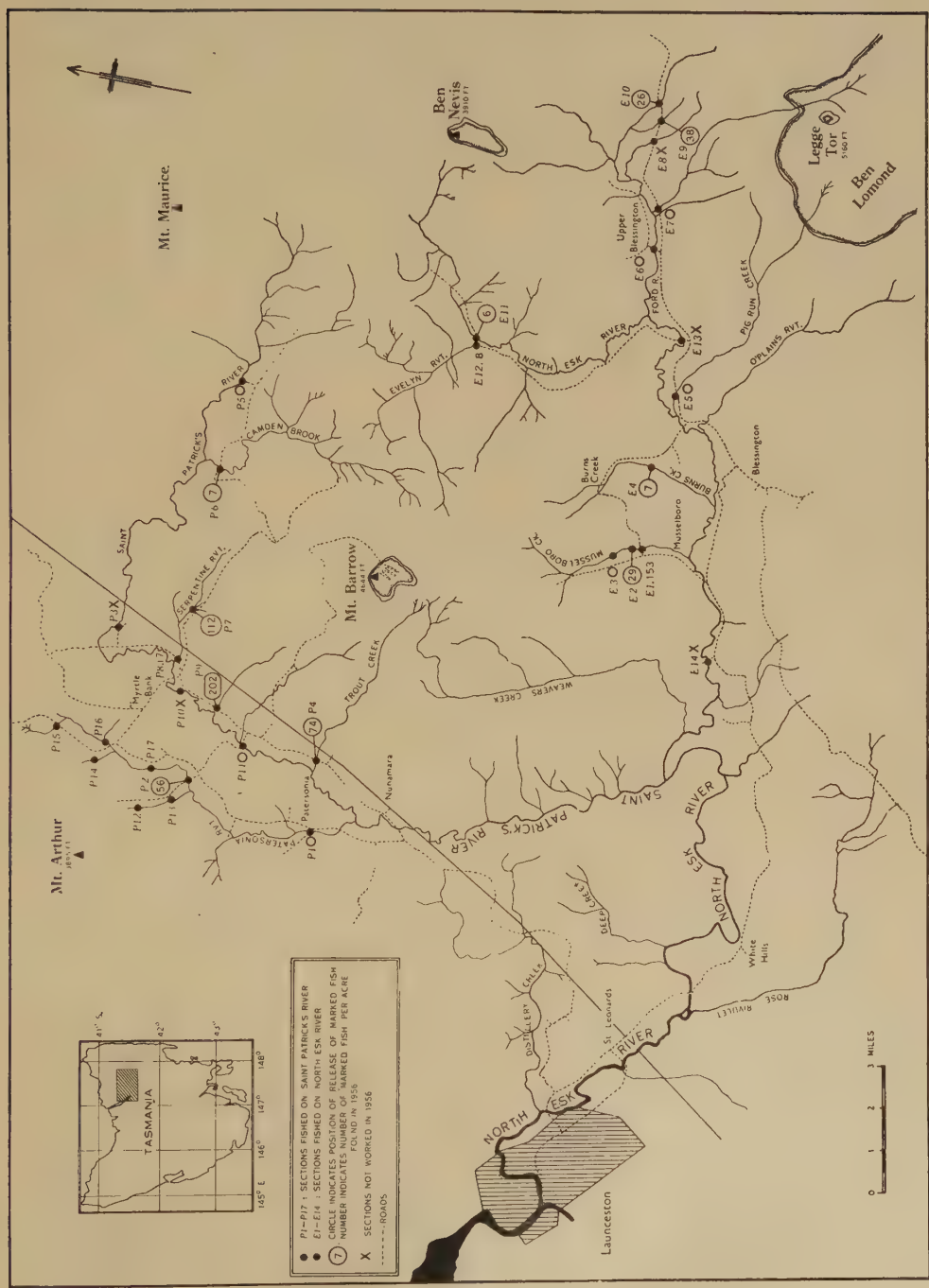

Fig. 1.—Map of North Esk River basin showing the positions of sections fished.

of the section fished was calculated and the results expressed to the nearest 5 sq. ft; all fish taken were measured and weighed and scales were taken for age determination.

Care was taken to ensure that as far as possible every fish in each section was captured. When using this method of fishing it has been noticed that occasionally fish are missed. One reason for this is that on initial contact with the electric field the fish makes a convulsive leap, possibly comparable with the "jerk" response described by Bary (1956), which brings it out of the water; on falling back, it may be carried downstream in the current and lost. Another cause of loss, in the case of a small fish, may be that, because of the failure to net it rapidly, it becomes "narcotized" and is carried away. Such cases are noted and by fishing the same section two or three times all such fish are usually accounted for. A proportion of the scale samples contained only replacement scales so that it was not possible to be certain of the age of such fish. On the basis of their lengths these were allocated to their probable age groups, with the possible introduction of a small error.

(*b*) *Efficiency of the Electro-fishing Method*

In a population study of a similar nature, Schuck (1945), using the electro-fishing apparatus of Haskell and Zilliox (1941), which has the effect of stunning the fish, found that there was a loss of efficiency in capture, increasing with decrease in fish length. This would appear to be related in part to the difficulty in seeing fish once they were stunned, and it is to be expected that small fish, stunned while hiding below the larger boulders of a stream bed, would not be seen. A similar test was carried out here using continuous D.C. which does not stun the fish. One section of a side channel of the Plenty River about 100 yd long was screened at both ends with fine-meshed nets. This stretch was divisible into four sections of alternating shallow riffles and deeper flatwater sections of approximately similar lengths. These were comparable with those studied by Schuck, but differed in that they were adjacent and the whole was continuous. Sections I and III were pools, up to 3 ft in depth, in which the stream bed was composed of solid rock and boulders of mixed sizes; the deep water was along one side and the bottom rose gradually to shallow water on the other; the width varied from 15 to 25 ft. Sections II and IV were shallow, with fast-flowing water; their average width was about 10 ft and their depth about 8 in.

The area was fished once to collect a sample of the population; 525 marked fingerling brown trout of mean length 5·6 cm (range 4·3–6·9 cm) were then distributed throughout the area. The three upper sections each received 150 fish, and the lowest 75. The following day the whole stretch was fished twice. Three of the largest fish taken were opened and their stomach contents examined: a 25-cm sand-fish (*Pseudaphritis urvillei* Cuvier & Valenciennes) contained four of the released fish; a 20-cm brown trout had eaten one; and a 22-cm trout contained only caddis and gastropod molluscs. On the basis of these deaths and of all the large trout captured on the second day an allowance of seven deaths from predation and one accidental death was made, reducing the total of the assumed population of released fingerlings to 517.

On the first fishing of the second day 242 (47 per cent.) of the released fish were recaptured, and held until the completion of the second fishing operation in which an additional 105 were taken, showing a total of 347, or 67 per cent., for two operations. This is the normal process which has been adopted in making such stream surveys in Tasmania. Several interesting facts emerged from this study. There was clear evidence of downstream migration within 24 hours of release. Contrary to the findings of Schuck there was considerable difference in the relative recovery between the two riffles and the two flat-water sections; the lowest numbers were taken from the shallower sections on both occasions, with very much lower recoveries on the second occasion, suggesting either much lower populations or much greater efficiency in recovery on the first occasion in the shallower than in the deeper sections. From section I, which received only 75 fish, 133 were recovered, showing that the downstream migration was quite considerable. The extent of this migration was estimated on the basis of an even recovery of 67 per cent. throughout the area, it being assumed that in each case about half as many fish remained as were actually recovered from each section. The result showed that 81 (54 per cent.) of the fingerlings had moved downstream from the upper riffle (section IV) to the deeper section below, raising the total population of section III to 231; of these 76 (33 per cent.) had moved down to section II, increasing its population to 226; of these, 129 (57 per cent.) had migrated to the lowest section (I) whose population was estimated at 199, an increase of 165 per cent. The most extensive migrations were clearly from the two shallower sections (II and IV) to the two deeper sections (I and III). This migration may have been stimulated in part by the relatively high rate of release but it shows what is likely to happen when a thousand or so fingerlings are released in one place; the urge to move downstream in search of less crowded feeding conditions exposes them to greater predation by the existing population. In the present case predation was not high because the area used for this experiment was a comparatively recently developed side channel of the main stream, not fully populated.

One other interesting observation emerged from this study, relating to the efficiency of the method. The stream bed in the deeper sections was composed in part of large boulders which provide greater depth and thus more shelter for small fish, and permit deeper penetration into this shelter than is to be found in the shallower riffles where the bed was of smaller, and thus more closely packed, stones. At the normal speed of fishing operation the electrode passes over such sections before the smaller fish have time to come from the depths, whereas allowing the electrode to rest on the bottom for 5–10 sec at a time frequently produced such fish although none had appeared when the electrode was passed over the top. It is over this type of cover that D.C. has an advantage over A.C. since there is no immediate stunning of the fish and they are able to come out of hiding. Herein, perhaps, lies the explanation of Schuck's finding no difference between recoveries from shallows and depths, since in the deeper sections his small fish would have been stunned and so be lost to sight, whereas those which were readily seen were near the surface, as would also have been those which were taken in the shallower riffles. It is unfortunate that this difference was not realized until section III was being fished for the second

time, otherwise the rate of recovery would probably have been much higher, especially in section I. It is probable that this has been the major cause of loss of efficiency in Tasmanian streams since the quick appearance of some small fish, probably those just beneath the surface boulders, has given the impression that the fish react rapidly and that the first-comers represent all that were there. The general conclusion holds, that for fingerling fish the approximate efficiency of the method using D.C. is about 67 per cent. where streams have been worked over twice.

Schuck (1945) gives figures of 50, 81, 92, and 95 per cent. recovery respectively for fish of ages 0+, 1+, 2+, and 3+ and older, presumably for one fishing operation. A correction made on the assumption that similar percentages of the remainder would be taken in a second operation, indicates a high efficiency of capture for fish over 1 year of age. In the present case there was also a loss of efficiency in the instrument itself, due to the poor conductivity of the water. The machine, designed to give 250 V and 5 A, was on this occasion working at about 200 V and 0·2 A; this is related to the poor content of dissolved solids in the stream, and it has been observed that in streams where greater amperage is recorded the holding efficiency is much greater.

(c) *Temperature and pH*

Measurements of temperature and pH were made on March 4, 1955, at a time when the water flow was almost minimal and when the air temperature would be close to the maximum for the year. Temperature was recorded to the nearest 0·5°C and pH was measured with a Lovibond comparator using glass standards. Readings were made between 0945 and 1711 hr, and the altitude ranged from about 1100 to 1700 ft. The time of day would have some effect on water temperatures at this time of year, but altitude appears to have had a greater effect. Temperatures ranged from 11·5 to 16·5°C, the majority being between 12 and 15°C, and pH ranged from 6·1 to 7·4, though all but three of the values lay between 6·8 and 7·2.

III. Results and Discussion

(a) *The Survival of Released Fish*

At each section the distance fished depended on the accessibility of the site from the road and the straightness of the stream bed, and varied from 150 to 560 ft, with an average of about 350 ft. The average width also varied, according to the size of the stream, from 5 to nearly 60 ft, the average being about 20 ft. The actual numbers of fish taken varied from 2 to 122 in 1954–55 and from 1 to 110 in 1956. The total number of fish taken from 25 sections in the first season was 981, of which 887 were brown trout and 94 were other species, mostly eels; on the second occasion the total for 20 sections worked was 632 fish of which 34 were other species. Of the 598 trout taken in this season only 75 were marked fish.

Table 1 shows the number of fish per acre in each age group in the two seasons, and the marked fish are separated from the resident population. North Esk sites are numbered *E1* to *E14*, and St. Patrick's sites *P1* to *P11*. Stream measurements and other basic data are given in Appendix I. The mean widths of nearly all sections of streams were greater in 1956 than in the previous season, as a result of the

TABLE 1

NUMBER OF BROWN TROUT PER ACRE IN 1955 AND 1956

Section No.	Age Groups												Totals		
	0+		1+				2+		3+		Older				
	1955	1956	1955	1956			1955	1956	1955	1956	1955	1956	1955	1956	
				Wild	Marked	Total								Actual	Corrected†
E1	0	51	72	17	153	170	202	102	101	102	58	0	433	425	461
*E2**	0	0	76	0	29	29	54	86	54	48	0	0	184	163	181
E3	0	10	129	69	0	69	117	138	12	39	0	10	258	266	293
*E4**	0	7	100	0	7	7	85	52	8	22	7	0	200	88	96
E5	0	11	82	0	0	0	265	90	163	146	112	90	622	337	299
E6	16	5	93	54	0	54	45	79	37	0	4	5	195	143	138
E7	0	0	18	15	0	15	128	30	0	30	73	0	219	75	88
E8	0	—	0	—	—	—	12	—	12	—	0	—	24	—	—
*E9**	0	5	29	16	38	54	70	49	100	33	0	0	199	141	170
*E10**	0	0	278	130	26	156	139	104	167	52	0	52	584	364	387
*E11**	0	0	39	14	6	20	79	26	0	13	0	6	118	65	69
E12	0	12	39	9	8	17	51	66	12	8	0	4	102	107	103
E13	6	—	39	—	—	—	51	—	21	—	24	—	141	—	—
E14	12	—	67	—	—	—	14	—	12	—	2	—	107	—	—
P1	5	99	262	33	0	33	97	113	29	14	5	4	398	263	281
*P2**	0	49	220	30	56	86	40	148	7	25	0	19	267	327	339
P3	0	—	3	—	—	—	6	—	6	—	0	—	15	—	—
*P4**	287	66	126	199	74	273	57	25	34	0	11	0	515	364	452
P5	0	0	0	?	?	4?	11	0	0	0	0	0	11	4	5
*P6**	0	7	0	13	7	20	12	0	19	0	0	0	31	27	31
*P7**	0	132	124	61	112	173	124	41	11	20	0	0	259	366	415
P8	38	484	633	50	17	67	268	217	173	67	29	33	1141	868	1107
*P9**	231	74	578	223	202	425	165	74	182	21	99	11	1255	605	811
P10	32	—	79	—	—	—	29	—	4	—	4	—	148	—	—
P11	10	15	42	45	0	45	52	30	10	15	0	5	114	110	119

*Positions of release of marked fish. †Corrected for error due to greater width of stream sections caused by unseasonal rise in river levels in 1956. Sections *E8*, *E13*, *E14*, *P3*, and *P10* were not fished in 1956.

temporary raising of the normal summer water levels caused by the heavy rain. Calculations of the numbers of fish per acre for most sections, based on 1956 levels, will yield lower populations than were actually present, and total numbers per acre have therefore been corrected proportionally to the difference between the mean width at each site in the two seasons. Using the corrected values given in Table 1 it is found that the difference in the total population at the 20 sites fished in both seasons represents a fall in the later season to the extent of about 18 per cent. This can be wholly accounted for by the normal mortality which would have occurred during the 2 months' delay before the sections could be fished in 1956. Allen's (1952) data show that the mean expected mortality for fish older than 1 year, in the 2 months at this time of year, is about 18 per cent.

Because this estimated fall represents a mean for all sections, at some of which the numbers of fish per acre were higher in the second season than in the first, it must be regarded as only approximate; it is further influenced by the varying numbers of young fish (0+ and 1+) present in each season (shown in Table 1 and discussed in Section III(*b*) below); if these are excluded in making this comparison the fall in numbers in the second season amounts to only about 13 per cent., so that mortality during the 2 months' delay is quite sufficient to account for the lower numbers found during the second season.

Comparison of individual sections shows increases in population between 1955 and corrected 1956 values at six sites only; *E1*, *E3*, *E12*, and *P2*, *P7*, *P11*, and with the exception of the last, all were at or close to points of liberation of hatchery fish. At four of these the increase was due to the presence in 1956 of 0+ or 2+ and older fish in greater numbers than in 1955, and at only two was there any indication that it might have been due to released fish. At *E1* and *P7* there were big increases in the numbers of 1+ fish, of which the majority were released fish, suggesting that at these two sites released fish had made a considerable contribution to the population. However, this is not necessarily the truth as it will be shown that the natural populations of 0+ and 1+ fish are not truly represented in these samples.

Of the 10,000 fish released only 75 were recovered. It cannot be assumed that these represent the whole of the survivors since it is certain that some had moved out of the area in which they were released. This is shown where two or more sites were adjacent, as at Mussellboro Creek (*E1*, *E2*, *E3*) and Serpentine Rivulet (*P7*, *P8*). In the first, trout having been released at the middle of the three sites would disclose whether there was migration in either direction, and at the second they were released at the upstream site. In both cases there was downstream migration. Sites *E1* and *E2* were less than half a mile apart, while nearly three-quarters of a mile separated *E2* and *E3*. Sites *P7* and *P8* were less than 2 miles apart. It is doubtful if the downstream migration exceeded 2 miles: no marked fish were found in the main stream at *P11*, less than 2 miles below *P9* which was still carrying a good proportion of these fish; neither were marked fish found at *P1*, some 4 miles below the point of liberation (*P2*) in Patersonia Creek; nor at *E6*, a little over 4 miles below liberations at *E9* and *E10*.

In estimating the total possible survival it has been assumed that the downstream dispersal tapered off steadily to zero at 2 miles below every point of

release. This may be inaccurate because although fish were released at *E2*, more were found at *E1* than at *E2*, but as pointed out above these two points were very close. For the purpose of estimating the survival in this stream, *E1* was taken as the point of release and the dispersal calculated on the assumption that the limits of dispersal were, downstream, 2 miles from *E1*, and upstream, as far as *E2*. On the basis of these assumptions it has been calculated that about 1100 marked fish could have survived from the end of June 1955 to the time of recapture; a period varying from 7 to 9 months. Thus the mortality suffered during this period would be nearly 90 per cent., compared with a mortality of about 50 per cent. for the natural population over the same period, based on Allen's data (1952). At normal rates, 30 per cent. could be expected to die during the remainder of that year, so that only about 400 would be likely to attain 2 years of age, and only 80 fish (0·8 per cent.) could be expected to survive to 3 years of age and reach maturity.

About 120 of the 400 fish would have been takable as 2-year old fish and the remainder not until they were 3 years of age, by which time they would have numbered only about 60. Thus, as a result of releasing 10,000 yearling fish in these streams, anglers could have expected an addition to the population of 120 takable fish in 20 miles of stream, 15 months after release, or six fish per mile in the 2-mile stretch below each of the 10 points of release; and during the following season they could have expected one of these to have survived and to be joined by an additional three fish per mile from the slower-growing fish. The normal population of takable fish in these 20 miles would have been about 1500. Direct evidence of the survival over 18 months in one section is provided by figures for section *P2* which was fished again in December 1956. The numbers estimated to have survived in the 2 miles below this point were 151 in March 1956 and 44 in December 1956, which shows a 4·4 per cent. survival for 18 months. The normal mortality rate for the next 6 months, at the end of which the fish would have been 3 years of age, is about 40 per cent., which would leave a total of 18 fish out of the original 1000, or 1·8 per cent. The growth rate at this site was such that the fish would be takable at this age, so that not more than 2 per cent. of the fish released here would survive to be available to anglers.

These results support the conclusions of Hazzard and Shetter (1939), Shetter and Hazzard (1941), Randle and Cramer (1941), Needham and Slater (1944), Hobbs (1948), and others. Needham and Slater (loc. cit., p. 34) state: "Fingerling trout of a practical size cannot possibly provide significant additions to the creel when they are planted in waters having abundant populations of resident trout" and "It can now be stated with confidence that by far the greater proportion of fish caught are the result of natural propagation".

Neither is any advantage to be gained by holding fish in the hatchery until they reach legal size, for although their mortality might be reduced, as Hazzard and Shetter (loc. cit., p. 206) discovered: "the consistent planting of a stream with legal-sized trout during the fishing season will eventually lower the number of adult trout of breeding size to a point where the contribution to the catch from natural spawning is seriously impaired" and "If carried to excess the result would be a

stream practically barren of trout except for those planted just prior to and through the season".

(b) *The Natural Population and its Mortality*

The percentage composition of the population at several selected sites in both streams, in two successive seasons, is shown in Figure 2. The only sites excluded are those with fewer than 15 fish taken in one of the seasons, and those which it

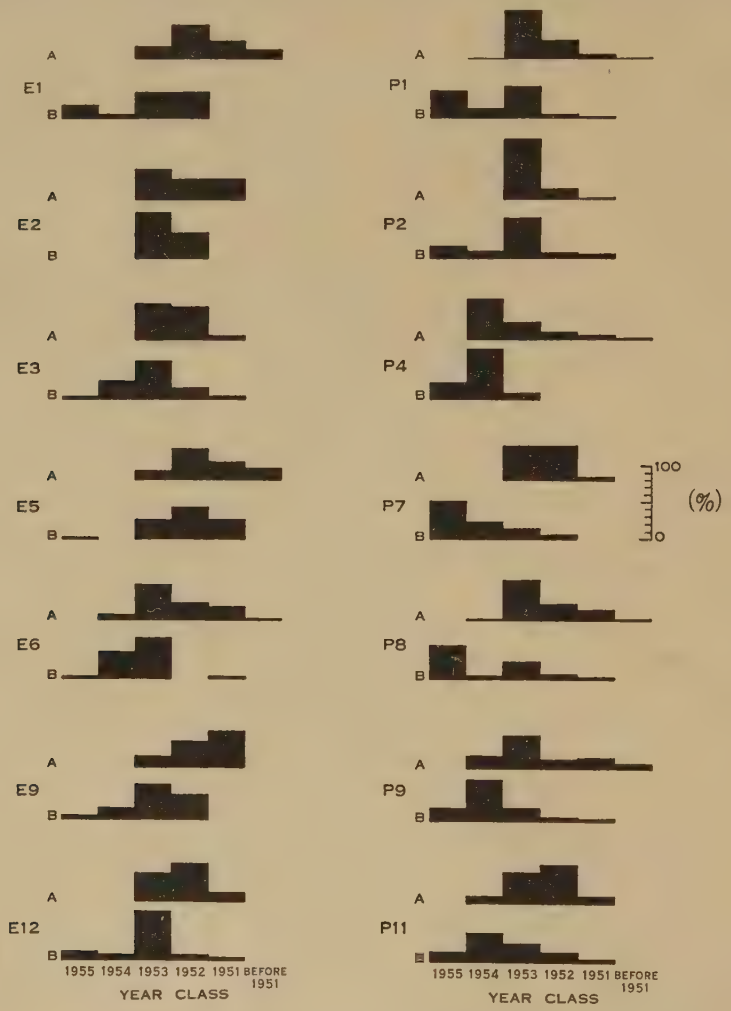

Fig. 2.—Percentage composition of the population at selected sites in two seasons: A, 1954–55; B, 1956.

was impossible to fish in the second season. This figure shows two important features. With few exceptions, in neither season was a normal distribution of the population found in any section; the majority of sections show populations greatly deficient in 0+ and 1+ fish. At *P4* in 1955 and *P7* in 1956 normal distributions were found which showed annual mortality rates constant at about 50 per cent.;

at *E6* and *P8* in 1955 and at *P11* in 1956 similar conditions were found, but 0+ fish were inadequately represented. In general there were fewer 0+ fish than 1+ fish in both the North Esk and St. Patrick's, and fewer 1+ fish than 2+ fish in the North Esk.

The second feature is that throughout the North Esk and in most of the St. Patrick's there were larger proportions of 1+ fish in 1956 than of 0+ fish in 1955, and the same relationship applies to the 2+ fish in 1956 and the 1+ fish in 1955 from which they arose. If this disproportion in numbers of fish in each age group had occurred in 1955 only, it would have appeared that there had been a failure in survival of that year class in both rivers, and of that of the preceding year also, in the North Esk. But since it is repeated in the second year, and especially in view of the increase in absolute numbers of 1+ fish in 1956 compared with the 0+ fish in 1955, this cannot be the explanation. It is clear that the population must be maintained by recruitment from nursery streams; these would be small creeks with sufficient flow of water in winter to permit fish ascending for spawning, but falling off in summer so that they were inhabitable only by the youngest fish. One such stream was found (Ration Tree Creek, Nicholls 1958*a*) in which the population was composed of 77 per cent. 0+ fish, 22 per cent. 1+ fish, and 1 per cent. 2+ fish. Its mean depth was 7·4 in. and its mean width was 14·3 ft, showing that it was a small shallow stream with a mean cross-sectional area of 8·8 sq. ft.

It would be expected, therefore, that the highest proportions of 0+ fish should be found in similar streams within the North Esk System. In the North Esk and its tributaries no small creeks less than 9 sq. ft in cross section are shown in Figure 2, and this subsystem was notably devoid of 0+ fish at most sites fished, but in the St. Patrick's tributaries four of the seven sites shown in Figure 2 had cross-sectional areas of 6 sq. ft or less, while the other three had areas from 30 to 40 sq. ft. The three largest (*P1*, *P2*, and *P11*) had very low or nil populations of 0+ fish in 1955, and of the four smallest (*P4*, *P7*, *P8*, and *P9*) two carried large populations of 0+ fish. These relationships were not so apparent in 1956, but the summer of that year was exceptional in that there were successive periods of heavy rainfall (Fig. 3).

To examine the possibility of recruitment from small streams, several sections in tributary creeks of Patersonia Rivulet, one of the larger tributaries of the St. Patrick's, were fished in December 1956. The upper site in this stream (*P2*) was fished as a control and several sections upstream from this position, or in minor creeks, were studied. The highest point reached was almost at the source of the main stream. The results are shown in Figure 4. In this figure the mean relative cross-sectional areas of the streams are shown diagrammatically, and the percentage distributions of the populations have been arranged in descending order of cross-sectional area. A very clear relationship now appears between the size of the stream and the proportion of young fish (0+ and 1+) in the population; it is clear that young fish are found in increasing numbers and proportions in the smaller and shallower creeks, and it is evident that such nursery streams are the source of recruitment to the stocks of older fish in the deeper sections. Saunders and Smith (1955) in a study of a population of brook trout, *Salvelinus fontinalis* (Mitchill),

found insufficient fingerlings to provide the stock of older fish, and concluded that the population was maintained by downstream migration.

At *P2*, although there was no real difference in numbers or weight of fish per acre in March and December 1956, the composition of the population was quite different. The numbers of the 1953 year class found on the three occasions this

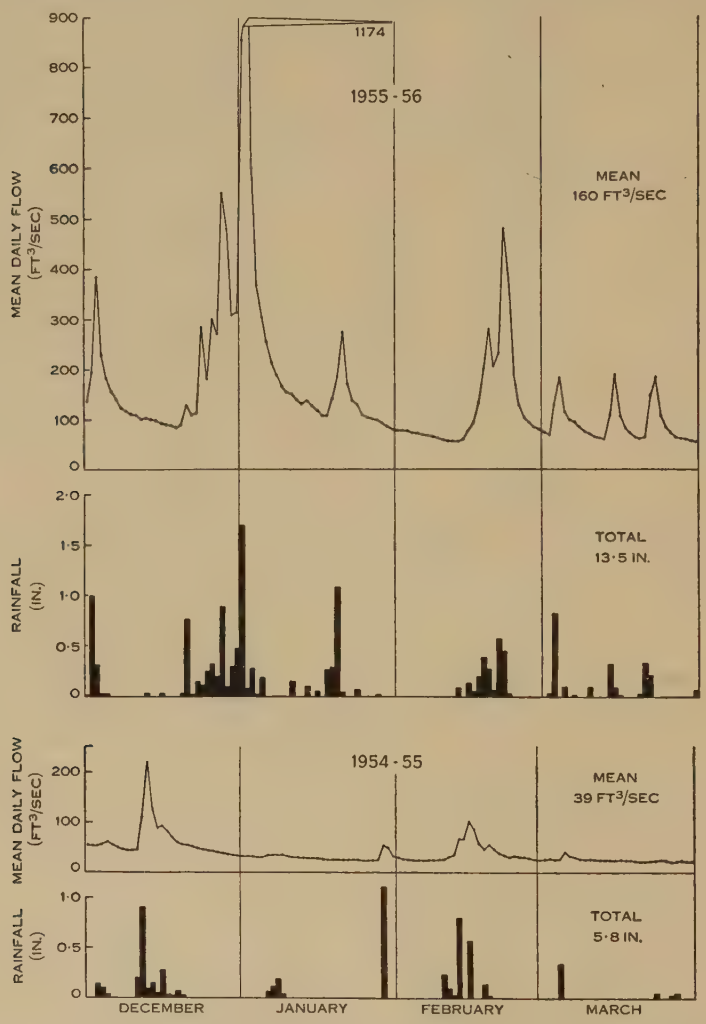

Fig. 3.—Rainfall and river flow in the North Esk River in two seasons.

section was fished were 220, 148, and 94 per acre, showing 33 and 36 per cent. mortalities; for the 1952 year class the corresponding figures were 40, 25, and 0 (38 and 100 per cent. mortalities). The 1954 and 1955 year classes showed increases in December 1956 over the numbers found in March of that year, showing that recruitment had occurred. *P12* and *P16* are omitted from Figure 4 because fewer than 15 fish were taken; at the others, numbers ranged from 38 to 83. *P17* was

upstream from *P2* in the main rivulet, and shows a greater number and proportion of 0+ fish than *P2*. *P13*, *P14*, and *P15* (especially the last which was near the source of the main rivulet) show the characteristics of a nursery stream similar to Ration Tree Creek, but all three showed the presence of a small number of older fish. The absence of 2+ fish from two of these sections, and their poor representation in the third, suggests that the older fish were not part of the normal resident population and their presence can best be explained on the assumption that they were either invaders from the main stream, which was quite close at both *P13* and *P14*, or mature fish which had remained upstream after spawning, at *P15*. Calculations based on Allen's (1951, p. 91) formula for egg production show that two

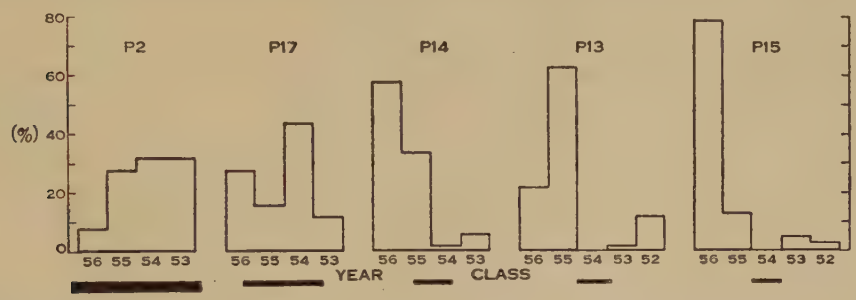

Fig. 4.—Percentage composition of the population by age in relation to stream size. The black areas beneath each site indicate the mean cross-sectional area of the stream drawn to scale.

4-year females about 30·0 cm in length and three 3-year females about 27·5 cm would have been able to produce the 30 0+ fish taken in the 70-yd section fished at *P15*, so that 10 mature fish were probably there in the winter; only three such fish were found and the other seven might have left the area or have been taken by anglers. No correction has been made for efficiency of the method and it is possible that the number of 0+ fish should have been higher, but although this section was fished only once it was relatively easy to fish and provided little or no deep cover for fingerlings.

Allen (1951) has shown that in the Horokiwi the average mortality rate after the first year is about 80 per cent. He also showed that fish in that stream made little or no spawning migration but tended to make their redds near where they were living. Schuck (1945) on the other hand was able to demonstrate an upstream migration in the spawning season, followed by a return "probably during the winter" to the sites from which these fish were originally taken. In Tasmania it has been shown that the average mortality rate in the rivers of the north-west is similar to that found in the Horokiwi (Nicholls 1958*a*) though in the North Esk it may be somewhat lower; there, it was tentatively estimated at about 70 per cent. on the basis of representation in anglers' catches (Nicholls 1958*b*). The mean mortality rates for older fish in all sections fished in the two seasons were 67 per cent. for 2–3 years of age, and 80 per cent. for 3 years to older fish. The alternative method of estimating mortality based on the survival from 1955 to 1956 of the 2+, 3+,

and 4+ fish (that is, the 1953, 1952, and 1951 year classes), for all sites that were fished in both seasons, yields mean values of about 60, 75, and 90 per cent. respectively. Such estimates involve the correction of the 1956 numbers for the difference in area due to the different river levels and for the mortality which would have occurred during the 2 months' delay in fishing. These results suggest that the average rate of 70 per cent. derived from anglers' catches is reasonably reliable. The increasing rates from the third year onwards found from the results of electro-fishing indicate a fairly heavy fishing intensity.

TABLE 2

ESTIMATED TOTAL POPULATIONS IN THE NORTH ESK AND ST. PATRICK'S RIVERS

Season	River	Age Groups			Totals	Total Takable
		2+	3+	Older		
1955	North Esk	16300	9000	3300	28600	14700
	St. Patrick's	10200	4400	1100	15700	6400
	Total	26500	13400	4400	44300	21100
1956	North Esk	17200	8800	2500	28500	15600
	St. Patrick's	13600	3200	1500	18300	7100
	Total	30800	12000	4000	46800	22700

(c) *The Total Population*

It is difficult to estimate the total population of this river system with reliable accuracy without a more comprehensive survey including many more sections of the stream and its tributaries. The nearest approach that can be made is to apply the average number per mile of all sections fished to an estimate of the total river distance measured carefully on the 2 miles to 1 inch map. This yields the figures given in Table 2, expressed to the nearest 100, in which the numbers of 0+ and 1+ fish have been omitted since they are not representative and are therefore of no significance, and the numbers of fish for 1956 have been corrected for the mortality which would have occurred during the 2 months' delay in fishing in 1956. The figures therefore represent the approximate numbers of fish estimated to have been present about January in both years. This method is not likely to exaggerate the estimate and can be regarded as minimal, since the length of the river must be underestimated when measured from a map. For example, the section worked at *P14*, a normal winding stream, measured 187 yd along the stream bed but the straight line distance between the two stop nets was 135 yd, showing that the distance, as measured on the map which shows this stream as a straight line, was underestimated by about 38 per cent. The average population per mile covers all sections of the river and includes populations of quite small numbers, so that the average may be regarded as fairly representative. However, this estimate is for those portions of the two rivers and their tributaries lying above section *E14* in the

North Esk and above the junction of the Patersonia Creek with the main stream in the St. Patrick's. Below these points lie many miles of better fishing water, stretches which were too deep to study with the available equipment. On the assumption that the populations of takable fish at *E14* and *P11*, the lowest points fished, were similar to that of the river below these points, and knowing the approximate distance from the points to Launceston, it is possible to estimate the population in this unfished section. In the first season there were 186 takable fish per mile at *E14* and 189 at *P11*; in March 1956 there were 154 at *P11*, and when this is corrected for the assumed 18 per cent. mortality, it becomes 188. A value of 190 takable fish per mile, for the 40 miles of river between Hobbler's Bridge in Launceston and the lowest points fished, gives an estimated total of 7600 fish. These may be added to the estimated 22,000 found above these points, making a total of 29,600 in January of each year. If mortality for the 4 months which had elapsed since the beginning of the season in September accounted for 35 per cent., under the existing 70 per cent. annual mortality for this river system (Allen (1952) showed about 42 per cent. for this period under an annual rate of 80 per cent.), then the total number of takable fish at the beginning of the season would have been about 45,500.

It is of interest to relate this figure to the estimated total catch given in the survey of the North Esk fishery (Nicholls 1958*b*, Table 11). These figures were subject to a relatively large standard error, but the average for the last 5 years was 20,000, again suggesting that it is fairly heavily fished, and that anglers normally remove about 44 per cent. of the takable fish available at the beginning of the season. The removal of these fish would be beneficial rather than harmful since it would make possible a better survival and better growth rate for those which remain. Allen (1951, p. 181) discussing mortality due to angling, shows that it may vary from 12 per cent. to 92 per cent. depending upon the intensity of angling, the higher figures coming from parts of the United States. A value between 30 and 40 per cent. would not be unexpected. The rate of removal by angling in this river might account for the lower than usual total mortality, around 70 per cent. per annum, indicated in the survey of the fishery referred to above and supported by the present study.

Some indication of the composition of the population in the 8 or 10 miles of the North Esk immediately below *E14* is given by the 163 fish taken by one angler who fished this section regularly during the 1949–50 season. This sample shows the presence of 4+, 5+, and 6+ fish in proportions which indicate a mortality rate around 70 per cent. Below the section fished by this angler larger fish might be expected. The composition of his catch during the early part of the season was such that the estimated total of 45,500 takable fish would be composed of 900 6+ fish, 3500 5+ fish, 7300 4+ fish, 27,000 3+ fish, and 7300 2+ fish. The actual numbers of 2+ and 1+ fish, assuming a constant mortality rate of 70 per cent., would have been 89,500 and 298,000 respectively. Allowing a 50 per cent. mortality from all causes during the fishing season, assuming 50 per cent. of the survivors to have been females, and knowing their approximate mean lengths at the end of the season, it is possible (using Allen's formula for egg production in relation to length (1951, p. 91)) to make a rough estimate of the number of eggs that could be expected to be spawned in the following winter, by which time the 2+ fish would have

become 3 years of age, and mature. This totals about 25 million, and if the estimated 298,000 survived to become yearlings the first-year mortality would be about 98·8 per cent., which is not improbable. It would seem that this estimate of takable fish at the beginning of the season, while probably on the low side for reasons given above, is nevertheless adequate to maintain the stock even when subject to the heavy fishing which apparently occurs, because of the slightly reduced mortality rates which result.

The error likely to be introduced by not sampling the lowest 40 miles of this river is one which would omit the larger and older fish, and since their reproductive capacity is large relative to their number, correction for this error would increase the number of eggs spawned and so bring the first year mortality closer to the expected 99 per cent. It is highly probable that the number of takable fish per mile would increase downstream progressively as the river widens and deepens.

(*d*) *The Standing Crop*

The term "standing crop" is used here as defined by Carlander (1950, p. 222) as "the total amount of fish present at a given moment". To evaluate this it is necessary to have a reliable estimate of the total population of any given stretch of water, and this has been the aim of the present study. As Carlander states, confirmed by evidence produced in Section II(*b*) above, "electric shockers and nets . . . may give a measure of the standing crop, but . . . these estimates are subject to considerable error". In the present case no attempt will be made to estimate the standing crop for the river system, but values calculated for each section studied are given in Table 3, expressed as the total weight of fish in lb/acre on each occasion that it was fished. There is an error due to inefficiency of the method, but since this applies to any significant extent only to fish of the youngest age group, which are the lightest, the error involved in estimating the standing crop without correction for these will be relatively small, and the estimates can be regarded as minimal. As shown in Table 3 the weights of brown trout ranged from 2 to 182 lb/acre at 25 sites in December–January 1954–55, and from 1 to 133 lb/acre at 20 sites in February–March, 1956. The average values in each season were 53 and 52 lb/acre respectively. The mean percentages of brown trout in the total fish population were a little over 90 in both seasons.

As shown in Carlander's (1950, 1953) summaries, the standing crop for trout streams so far studied ranges from 0 to over 300 lb/acre. Some of those relating to brown trout may be quoted for comparison with values found here. Shetter and Hazzard (1939) in a study of eight sections in three streams in Michigan over a period of 4 months (June to September) found values for total fish populations ranging from 4 to 177 lb/acre; in these streams up to 11 different species of fish were found including crayfish, and brown trout in competition with brook and rainbow trout comprised only from 0 to about 70 per cent. of the total weight per acre. The weights of the standing crops of brown trout alone ranged from 0 to about 17 lb/acre, and of all trout from about 1 to about 40 lb/acre. These authors found that the carrying capacity of the streams was related to depth of water rather than

to the nature of the bottom or of the cover. Schuck (1945) found an average value of nearly 14 lb/acre for brown trout in 13 sections of a stream in New York State, based on samples taken in September over a period of 4 years. Stefanich (1952) obtained September values for brown trout of 37·5 lb/acre in a Montana stream.

TABLE 3

NUMBERS AND WEIGHTS PER ACRE OF ALL FISH, AND MEAN LENGTHS-FOR-AGE OF TROUT

Section No.	Number of All Fish per Acre		Weight of All Fish (lb/acre)		Mean Lengths-for-Age (cm)					
	1955	1956	1955	1956	L_1 1955	L_1 1956	L_2 1955	L_2 1956	L_3 1955	L_3 1956
E1	476	476	154 (8)*	150 (17)	9·5	8·4	17·9	19·0	23·1	25·9
E2	196	173	56 (4)	75 (4)	10·5	10·6	20·3	20·4	24·6	24·5
E3	257	266	34	56	8·2	7·0	17·5	15·9	20·5	21·0
E4	215	134	60 (3)	62 (18)	9·6	9·3	20·5	20·2	26·5	25·0
E5	622	337	111	77	6·8	6·5	13·8	13·5	18·1	17·7
E6	195	143	60	61	10·9	10·6	22·4	22·5	25·0	28·5
E7	385	133	96 (14)	39 (8)	10·8	10·8	19·8	19·0	25·0	24·0
E8	24	—	5	—	7·0	—	12·5	—	19·0	—
E9	199	141	36	24	8·1	6·8	14·9	14·4	19·6	19·6
E10	584	364	61	67	6·6	7·1	14·3	12·9	18·7	17·8
E11	118	65	19	16	7·6	7·6	16·8	15·1	—	20·0
E12	105	120	17 (3)	30 (3)	9·1	9·2	18·6	18·5	22·3	23·8
E13	150	—	58 (3)	—	10·7	—	20·7	—	25·9	—
E14	138	—	38 (9)	—	12·1	—	23·2	—	28·1	—
P1	524	277	111 (43)	55 (6)	9·1	9·2	17·5	17·0	21·9	24·8
P2	287	339	34 (4)	63 (3)	8·7	8·3	15·9	16·0	20·0	20·9
P3	51	—	14 (5)	—	10·5	—	22·4	—	26·0	—
P4	528	389	32	36 (4)	7·2	8·3	15·3	17·0	19·0	—
P5	14	4	3 (1)	1	9·8	—	17·8	—	—	—
P6	37	27	18 (1)	3	11·0	5·5	19·3	—	22·5	—
P7	270	386	46 (<1)	59 (1)	8·8	9·0	16·7	16·6	—	21·5
P8	1170	918	143 (4)	105 (10)	7·8	7·8	15·4	15·1	19·7	19·8
P9	1288	605	186 (4)	90	6·8	7·5	14·8	14·7	20·1	20·5
P10	166	—	28 (3)	—	9·8	—	19·5	—	25·0	—
P11	136	116	36 (11)	35	10·4	10·4	20·3	20·7	24·3	26·4

*The numbers in brackets are the weights in lb/acre of fish other than brown trout (mostly eels) included in the total weights of all fish per acre.

Values for all trout (brown and rainbow) sampled in 7 months during a period of 16 months ranged from 44 to 68 lb/acre, comprising from 28–80 per cent. of the total fish population. While the total weight of fish per acre found in various sections of the North Esk System is below the middle of the range so far reported for trout streams, in all cases where a comparison has been made with streams in different

parts of the United States, the weights of the total populations show a good standard and the percentage of trout in these populations is very high.

(e) *Length and Weight of Trout in Relation to Population Density*

Consideration of the results obtained by Cairns (1942), Frost (1946), Hartley (1948), Allen (1951), and Burnet (1952) leads to the conclusion that the short-finned eel, *Anguilla australis* Richardson, which occurs in this river system is a competitor with trout for food. This must therefore be included in any assessment of the effect of population density on the growth of trout. Table 3 shows the numbers and weights of all fish taken from each section, together with mean lengths-for-age of trout at the end of their first three winters, in both seasons. Statistical analysis shows that the results for the two seasons can be pooled to give mean values representing the growth of fish in each section; it also shows highly significant differences within age groups between sections.

If mean lengths are plotted against population densities for individual samples it is found that while there is some scatter there is at the same time a general trend in which lower mean lengths are associated with greater population densities. Because of this scatter the trends are more clearly seen when the samples are grouped. The sites have been arranged in ascending order of mean L_1 values in Table 4. These have been grouped so that there is no statistically significant difference between mean L_1 values within each group. Mean L_1 values and mean numbers of fish per acre have been calculated for each group and if these are plotted they show that a curvilinear relationship exists between the length of fish and density of population. If L_2 and L_3 mean values are plotted a similar relationship is found. For L_2 values the groups are not homogeneous and statistical analysis shows that the differences within each group are quite significant for Groups II, III, and IV, and at the 5 per cent. level for Group I. These groups can be subdivided into two or more subgroups, but owing to the considerable variation in length at the end of the first winter, grouping the L_2 values for mean lengths loses some of its significance. Growth rate is shown more accurately by considering the percentage increments from L_1 to L_2, and if these are calculated for each section it will be seen that within each group there exist subgroups with different growth rates. These are shown in Table 4 together with the mean L_2 values for each subgroup. Statistical analysis shows no significant difference in the mean lengths within subgroups. When mean population densities are calculated for each subgroup it is found that the lower percentage increments from L_1 to L_2 within each subgroup are consistently related to a higher population density. If it is attempted to carry this analysis to L_3 values it is found that owing to the spread of these values, and the few fish in many samples, no statistically significant difference is found within each group. The percentage increments from L_2 to L_3, which vary from 16 to 52, can be used to arrange the samples in further subgroups which bear a relation to the mean population density for those samples within each group.

There is one obvious exception to this general trend, in which the fish at *E8* were among the lowest size-group at the end of their first winter and showed the lowest percentage increment recorded, and yet they numbered only 24 fish to the

TABLE 4

GROWTH OF FISH AND POPULATION DENSITY

Group No.	Section No.	Mean L_1 (cm)	Group Means		Sub-group No.	Section No.	Mean L_2 (cm)	Percentage Increment L_1 to L_2	Mean Percentage Increment	Subgroup Means		Group Means	
			L_1 (cm)	No. of Fish/Acre						L_2 (cm)	No. of Fish/Acre	L_2 (cm)	L_3 (cm)
I	*E5*	6·7	6·9	547	I*a*	*E8*	12·5	79	79	12·5	24	13·9	18·5
	E10	6·8			I*b*	*E5*	13·7	104	104	14·0	633		
	E8	7·0				*E10*	13·8	103					
	P9	7·2				*P9*	14·7	104					
II	*E3*	7·6	7·8	405	II*a*	*E9*	14·7	88	94	15·1	558	15·5	19·8
	E11	7·6				*P8*	15·3	96					
	P8	7·8				*P4*	15·8	98					
	E9	7·8			II*b*	*E11*	16·2	113	115	16·4	177		
	P4	8·0				*E3*	16·5	117					
III	*P2*	8·5	9·0	262	III*a*	*P2*	16·0	88	88	16·8	347	17·8	23·2
	P7	8·9				*P7*	16·7	88					
	E1	9·0				*P1*	17·3	88					
	E12	9·1			III*b*	*E1*	18·2	102	105	18·9	199		
	P1	9·2				*E12*	18·5	103					
	P6	9·2				*P6*	19·3	99					
	E4	9·5				*E4*	20·4	115					
IV	*P5*	9·8	10·5	143	IV*a*	*P5*	17·8	82	82	19·1	134	20·8	25·4
	P10	9·8				*E7*	19·5	81					
	P11	10·4			IV*b*	*P10*	19·5	99	95	20·4	156		
	P3	10·5				*P11*	20·4	96					
	E2	10·6				*E2*	20·4	92					
	E13	10·7				*E13*	20·7	93					
	E6	10·8			IV*c*	*P3*	22·4	113	111	22·5	130		
	E7	10·8				*E6*	22·5	108					
V	*E14*	12·1	12·1	138	V	*E14*	23·2	92	92	23·2	138	23·2	28·1

acre. Only two fish were found at this section in 1955, one 2+ and one 3+, and in 1956 this creek was not worked because it carried no water. It is probable that it had been diverted for irrigation, sawmilling, or other purposes and could not be regarded as a typical stream inhabitable by trout, and may be omitted from further consideration. It will be seen that although, when the sections are grouped as in Table 4, the growth shows a relationship to the mean number of fish per acre for each group, these means are based on figures which themselves show some variation, and the largest populations do not necessarily fall into the group with the lowest growth rate. Station *P8*, for example, had a higher mean population for the two seasons than did *P9*, yet growth was better at *P8*; similarly *P6* with quite a low mean population did not show such good growth as *E4*, *E6*, or *E7*, with higher population densities. Clearly other factors are concerned here and without going

TABLE 5

MEAN NUMBER AND MEAN WEIGHT OF FISH PER ACRE

Grouped Numbers of Fish per Acre	Mean No. of Fish per Acre	Mean Weight of Fish (lb/acre)	No. of Samples in Group
1–100	31	9	7
101–200	145	43	17
201–300	259	46	7
301–400	354	67	5
401–500	445	136	3
501–600	545	87	3
601–700	622	111	1
over 1000	1095	165	2

into detail as to the reasons, presumably related to food production for which no data are available in this study, it should be possible to discover which sections showed the best conditions for trout growth. Light is thrown on this question by a study of the weight of fish per acre in relation to population density.

Table 5 shows the mean number of fish per acre for arbitrary groups and the corresponding mean weight of fish per acre. Since the 0+ fish vary in their proportional representation and contribute only an insignificant amount to the weight, these have been excluded. Within each group there is considerable scatter, with a general upward trend shown only in the groups for 1–100 and 301–400 lb/acre. When the means are plotted there is relatively little scatter and the points lie about a straight line with a suggestion of curvilinearity. One point only lies far off the curve, that for the mean value of 445 fish per acre with an unduly high value of 136 lb/acre. This group contains section *E1* in both seasons, and *P8* in 1956, and it is the former which is responsible for the high value. In both seasons the number and weight per acre were remarkably close, averaging 450 fish per acre and 152 lb/acre. The stream at this point deepened into a large pool as it passed under a

bridge. It may be stated that, in general, there is a close relationship between the number and weight of fish per acre.

(*f*) *The Condition Factor*

Condition factors have been calculated for each fish, and means for all fish of each age group. Comparison of the values within age groups and sections between seasons showed that in most cases there was no reason why they should not be pooled. As between sections, and as between age groups within sections, there is considerable variation and this is best shown by grouping sections with similar values. Because the 2+ fish were the most numerous they have been used as the basis for grouping, and sections have been arranged so that there is statistically no significant difference

TABLE 6

GROUPED MEAN K VALUES FOR FISH OF EACH AGE GROUP

Group No.	Section No.	Age Groups			
		1+	2+	3+	4+
I	*E12, E14*				
	P5, P11	1·19	1·06	1·10	1·08
II	*E1, E6*				
	P1, P2, P3, P4, P6, P7, P8, P10	1·25	1·17	1·12	1·09
III	*E2, E3, E4, E5, E7, E9, E10, E11, E13*				
	P9	1·34	1·26	1·17	1·11

between the mean values for 2+ fish within a group. Under this arrangement there is no significant difference between the means within any age group except for the 1+ fish in Group I and the 4+ fish in Group III, which show differences significant at the 1 per cent. level. The grouped mean values are given in Table 6.

When the values for fish of the same age are compared as between groups highly significant differences are found for 1+ and 2+ fish; differences significant at the 1 per cent. level for 3+ fish; and no significant difference for 4+ fish. The variation shown in fish from different sections is therefore probably real. If fish of different ages are compared within groups, highly significant differences are found in Groups II and III, and at the 1 per cent. level in Group I, indicating that the observed fall in condition with increasing age is also real.

A comparison between the resident and released fish at sections of release shows that the former had a much higher mean K value (1·38) than the latter (1·20) in the North Esk; in the St. Patrick's the difference was smaller (means: 1·20 and 1·10 respectively). Klak (1941) has drawn attention to the fact that in certain Virginian streams, although released fish were of the same average length as the

native fish of the same species, the condition of released fish was considerably lower than that of resident fish over a period of 4 years. He concludes (loc. cit., p. 285) that "hatchery fish are handicapped, even when planted as fingerlings in streams exceptionally rich in food, because hatchery conditions prevent them from perfecting their natural foraging ability".

(*g*) *Population Density and Total Weight in Relation to Volume of Water*

Shetter and Hazzard (1939) in a similar study noted that, in general, shallower shaded sections with submerged cover produced the greatest number of 0+ fish, and that an average stream depth of 14 in. or more was the only habitat characteristic that could be definitely correlated with a greater than average population of trout and other fish. Schuck (1945) found greater numbers of larger fish present in areas of greater depth and volume of water, and greater numbers of fingerlings in sections with greater velocity and area, the large fish being defined as those of 3–5 years of age. This did not prove to be the case here; no correlation existed even when the sections were arranged in two groups: those with mean depths greater or less than 14 in. The shallower sections had a mean value of 80 per cent. younger fish and 20 per cent. older, and those with greater depths and volumes had mean values of 78·5 and 21·5 per cent. respectively, showing differences too small to be regarded as significant.

This difference in the results is probably due to the very different growth rates found in different parts of this system, so that "larger" fish are not necessarily equivalent to older. It would seem better to use the size limit of 9 in. as the criterion, and when this is done the expected result is found, with mean values of 18 per cent. larger fish in the shallower sections and 40 per cent. in the deeper sections.

It seems that in the North Esk System takable fish are distributed throughout but are found in increasing proportions downstream. The only large fish taken in this system (a 21-in. fish weighing $3\frac{1}{2}$ lb) was found at the lowest section fished, where the stream was at its widest. The mean weights of trout for these two groups were 75 and 30 lb/acre respectively. It is of interest to note that the mean numbers of eels were the same in both groups, showing a relatively greater ratio to trout in the deeper sections, and their respective mean weights were 3 and 7 lb/acre, indicating an increase in size in the deeper waters. Since accessibility from the road was essential because of the heavy equipment, it may be expected that in most cases the sections fished were also those most heavily angled. This would result in estimates of the population being lower than in the less accessible reaches and it is probable that the figures given here are minimal on that account. Only a few sections were heavily overgrown with vegetation and at one in particular (*E5*), which was difficult to fish, the number of fish per acre was the highest in the North Esk. Only two other sites exceeded the number taken here; they were in the St. Patrick's (*P8* and *P9*) and although there was less cover for fish, conditions were not good for angling. This agrees with the findings of Needham, Moffett, and Slater (1945) who found a much greater population of trout in a section of river closed to angling than in a comparable section which was open to angling.

IV. Conclusions

In the stream survey described by Schuck (1945) the extent of the loss due to inefficiency of the method was known and appropriate corrections were applied to the number of fish caught; from these Schuck estimated annual survival rates for fish from 0 to 5 years of age and over, including mortality due to angling. From these figures the mortality rates were approximately 76, 54, 50, 77, and 62 per cent. respectively, and are comparable with the figures given here which include angling mortality. By maintaining a controlled creel census over the period of the investigation he was able to show that angling was responsible for the greater mortality of the older age groups. He was also able to demonstrate that mortality among takable fish due to angling accounted for only about 15 per cent. of the total, and that a considerable natural mortality in these fish occurred during the summer, not traceable to any obvious cause. This mortality due to angling is close to the value found by Allen (1951) for the Horokiwi, but must also be related to the intensity of fishing. Although no reliable data are available to indicate the intensity of fishing in the North Esk System, the mortality due to angling is probably about 40 per cent.

Schuck's estimate of the total population in the 4·17 miles of stream studied shows about 625 fish per mile compared with the average value of 600 in the North Esk (no allowance has been made here for inefficiency of the method). No comparison between numbers of takable fish is valid since the size limit in Crystal Creek was 7 in. compared with 9 in. in Tasmania. Schuck also derived certain conclusions regarding the survival of fingerlings released from a hatchery into this stream; he found a maximum of 6·3 per cent. survival over 1 year compared with 24·1 per cent. for wild fish of the same age; the results presented here show close agreement in that the survival over 9 months was estimated not to exceed 11 per cent. Comparable figures for the survival of the natural population over that period are not available because they were not truly represented in the catches. That this is so is shown quite clearly from the actual capture of fish from section *P2* on two successive occasions. In March 1956, 9 months after liberation, the number of 1+ fish per acre was 86, of which 55 were marked; in December of the same year the corresponding numbers of fish, which were now 2+, were 94 and 17 respectively. These figures show that while there had been a mortality of nearly 70 per cent. among the marked fish during the 9 months, there had been an increase in the numbers of resident fish to the extent of nearly 150 per cent., indicating extensive recruitment.

The results of this study clearly indicate that in the North Esk System some fish spawn in the deeper and wider sections, but that where they do so the mortality suffered by the young is greater than normal and too high to permit any real contribution to the stock or to enable them to maintain the population of takable fish at the level at which it is quite clearly existing. Greeley (1932) has discussed mortality at spawning, and this is further considered in Appendix II. The main source of fish to maintain the stock must come from the numerous shallow tributary creeks and the headwaters of the system, where the numbers of young fish have been shown to be greatly in excess of those required to produce the numbers of older fish found there—a reversal of the conditions found in the downstream sections.

Inefficiency of the method cannot account for the small numbers of young fish found in most of the sections fished in 1954–55, and the increased proportions of young fish found in 1956 indicate that there had been a downstream migration, probably related to the heavy rainfall which occurred in that season.

Downstream movement of fish has been demonstrated by a number of workers. Cooper (1953) showed it to exist in released fish and to be closely related to temperature, occurring only when that was below 50°F. Needham and Cramer (1943), using a two-way fish trap, also demonstrated a strong downstream movement with no apparent correlation with water temperatures, but taking place in spring and coinciding with rising, but not maximum, stream flows; lack of food and shelter were suggested as factors responsible for the migration. It will have been noted that the downstream migration of young fish which had occurred by February 1956 was associated with rising river levels, but it is probable that in normal years this takes place towards the end of summer, or with the first rains of autumn.

Needham and Slater (1944) have shown that under certain conditions it is possible to anticipate the success of releasing trout when the weight of the resident population of trout is known. This is based on the known survival rate of released fish, but since in their case the fish were released into individual screened sections of experimental streams accurate figures for survival could be obtained because no fish could escape. In the present case the fish were released into open streams and were free to move; that they did so has been shown. It is, however, possible on the basis of the estimated survival for each 2-mile section over which they were assumed to have dispersed, to compare the numbers of fish surviving in such sections with the total resident populations of all fish in these sections. These figures are given in Table 7. If these pairs of figures are plotted it appears that a relationship exists whereby the higher the resident population the better the survival of released fish, which suggests that the resident population is already making good use of the available food but that the stream is able to carry additional trout to the extent of about 14 per cent. of the resident population.

Each of the population factors which has been considered in the study of these streams seems to have contributed something to the question of the ability of each section to support fish. It has been seen that some sections carried very few fish; that in some the released fish showed a better survival than at others, and that growth rate and condition also varied from place to place, and it may have appeared that some of these streams could be restocked to advantage. It seems then that consideration of these factors together, for each separate site, should give a reliable measure of stream conditions and show whether additional stocking in some places might be of value. For this purpose 2-year fish will be used for the assessment of growth and condition, since they predominated in every case.

The results of such an analysis can be summarized as follows: in the North Esk, *E1* and *E5* appear to be good sections of stream carrying large numbers and weights of fish per acre, but, because either the length or the condition was below average, they are considered to be fully stocked. *E2*, *E3*, *E4*, *E6*, *E7*, *E9*, *E10*, *E13*, and *E14* are all moderately good sections, apparently fully stocked, and at only one of the places where fish were released did the absorption exceed 16 per

cent. of the resident population. At *E2* it amounted to 37 per cent. and the implication that this section could have carried more fish is supported by both length and condition which were above average; *E13* and *E14* could also probably have carried more fish. It is clear that these sections would have been repopulated by downstream movement of fish. *E8*, *E11*, and *E12* are poorer sections, with relatively low numbers and weights of fish per acre, and the below-average lengths and condition factors suggest that they were fully stocked.

TABLE 7

RESIDENT POPULATION AND SURVIVAL OF RELEASED FISH

Section	No. of All Fish in 2 Miles	No. of Survivors in 2 Miles	Survivors (%)
P6	150	21	14
E11	240	13	5
E4	480	14	3
E9	670	104	16
E10	700	26	4
E2	870	318	37
P7	880	148	17
P4	1100	116	11
P9	1100	220	20
P2	1700	151	9

In the St. Patrick's, *P1*, *P8*, and *P9* are regarded as good sections, carrying above the average in numbers and weights of fish per acre, but since the lengths or condition factors tended to be below average it is concluded that they are fully stocked; *P9* absorbed released fish to the extent of 20 per cent. of the resident population. *P2*, *P4*, *P7*, *P10*, and *P11* are moderately good sections carrying about average numbers and weights of fish per acre, and as lengths and condition factors tended to be low, these are considered to be fully stocked. *P3*, *P5*, and *P6* are considered to be poorer sections in which the numbers and weights per acre were all quite low; the length was below average (except at *P6*) and the condition was average to low. The facts suggest that these sections were fully stocked; the absorption of released fish at *P6* was equivalent to 14 per cent. of the very low resident population. Those sections which carried very low populations and at first sight might appear to be in real need of restocking have all been shown to be poor sections, probably incapable of carrying larger stocks of fish. These observations are based on conditions during the middle of the season, at which time the stock has been depleted by angling and the normal downstream migration of young fish has not yet taken place, so that any deficiencies in the population apparent at that time would be made good later in the year by natural means. It has been shown that stocking with hatchery fish is of little value in these streams.

Of considerable practical interest here is the extent of the protection afforded to fish by the application of the 9–in. size limit. It is clear that as any year class ages its weight increases but its numbers decrease. Allen (1951) and

others have shown that the optimum time to crop a stock is when the weight of any particular year class is at its maximum. From the mean weights of fish of each age taken at each site during this survey, and assuming a 70 per cent. annual mortality after the first year, the total biomass of each age group has been calculated for each site. This shows, rather surprisingly, that for the 22 sites for which data were available the 1+ age group had a greater mass than the 2+ at 17 of the

TABLE 8

TOTAL WEIGHTS OF FISH PER ACRE AVAILABLE TO ANGLERS UNDER DIFFERENT SIZE LIMITS

Section No.	Total Weight (lb/acre)		
	Size Limit		
	9 in.	8 in.	7 in.
E1	98	130	140
E2	31	39	42
E3	5	10	24
E4	32	42	44
E5	30	52	76
E6	48	49	50
E7	59	76	81
E9	6	19	29
E10	2	16	33
E11	0	4	13
E12	4	9	12
E13	41	47	51
E14	18	19	24
P1	17	32	41
P2	1	4	9
P3	8	9	9
P4	5	10	17
P5	1	2	3
P6	17	17	17
P7	5	13	28
P8	21	47	75
P9	72	99	122
P10	8	12	17
P11	13	18	20

sites; they were about equal at 3 sites; and the 2+ had the greater mass at 2 sites. In every case the biomass of the 2+ fish was greater than that of the 3+ fish. This suggests that for most of the sections of river examined the optimum time to fish the population is during the second year of the fish and that there is considerable wastage of fish because anglers are unable to retain the younger fish owing to the imposition of the 9-in. size limit. These calculations have been based on the lengths and weights of fish measured at about the middle of the growing (and

angling) season, so they may be regarded as representing average conditions for the season. Because increase in weight is more rapid than increase in length they distort the relationship in favour of the 1+ fish when compared with conditions at the beginning of the season, but correspondingly they fail to do justice to the same fish when taken at the end of the growing season.

In places where the population was dense and the growth rate was low there is a case for a reduction of the size limit. Allen (1954) has discussed the effect of size limits on the yield and his Figure 4 is a chart from which the protection afforded by different minimum lengths may be estimated for fish over a range of lengths. Knowing the mean lengths of fish of each age group and using his chart to estimate percentages takable, the total weight per acre of fish available to anglers, based on the actual occurrence of such fish in each section, has been calculated, and the figures are given in Table 8 for the existing 9-in. size limit and for 8-in. and 7-in. size limits. The figures show that in sections where growth was good, or the population was sparse (as at *P6*) little addition to the available weight is made by reducing the size limit, but where growth was poor or the population was dense, considerable relative increases in the weight available to anglers follow. The averages for the 24 sections included in this Table show a 43 per cent. overall increase as a result of a reduction of 1 in.; and an 80 per cent. increase if it were reduced to 7 in. A reduction in the size limit would thus give anglers the benefit of fish which would otherwise be wasted to natural mortality. It is to be noted that very considerable increases occur where the population is densest and it is to be expected that the effect of lowering the size limit would be to thin out the population and thus enable a better growth for the remainder, though, as Allen (1954) has shown, the relationship is not direct but is dependent on a number of other factors.

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Appendix I

Table 9

BASIC DATA FOR 1954–55

Section No.	Name of Stream	Date	Length of Section (ft)	Mean Width (ft)	Mean Depth (in.)	Number of Fish Taken			Weight of Fish Taken (lb)		
						Brown Trout	Eels	Other Species	Brown Trout	Eels	Other Species
E1	Musselboro Creek	2.xii.54	195	15·4	11·1	30	3	—	10·16	0·53	—
E2	Musselboro Creek	3.xii.54	278	14·4	9·5	17	1	—	4·72	0·38	—
E3	Musselboro Creek	6.xii.54	252	14·8	9·8	22	—	—	2·94	—	—
E4	Burns Creek	7.xii.54	402	14·1	7·5	26	2	—	7·33	0·41	—
E5	Pig Run Creek	8.xii.54	324	13·2	9·2	61	—	—	10·88	—	—
E6	Ford River	9.xii.54	384	28·0	12·8	48	—	—	14·70	—	—
E7	Phillip's Creek	9.xii.54	450	5·3	6·3	12	9	—	4·50	0·75	—
E8	Unnamed Creek	10.xii.54	288	12·6	5·9	2	—	—	0·39	—	—
E9	Ford River	10.xii.54	399	18·7	5·8	34	—	—	6·22	—	—
E10	Unnamed Creek	10.xii.54	204	7·7	5·1	21	—	—	2·19	—	—
E11	North Esk River	17.xii.54	432	15·4	12·9	18	—	—	2·91	—	—
E12	Evelyn Rivulet	17.xii.54	404	29·1	13·0	26	1	—	3·69	0·75	—
E13	North Esk River	20.xii.54	369	39·4	17·0	47	3	—	18·38	1·03	—
E14	North Esk River	21.xii.54	426	57·7	20·2	61	17	—	16·44	4·88	—
P1	Patersonia Rivulet	13. i.55	384	23·3	14·6	82	24	2*	14·09	8·65	0·13*
P2	Patersonia Rivulet	14. i.55	301	21·7	18·3	40	3	—	4·52	0·56	—
P3	St. Patrick's River	17. i.55	324	42·4	18·1	5	11	—	2·94	1·44	—
P4	Trout Creek	18. i.55	366	10·4	7·2	45	1	—	2·77	§	—
P5	St. Patrick's River	19. i.55	360	43·4	11·3	4	—	1†	0·91	—	0·25†
P6	Camden Brook	19. i.55	306	22·1	18·8	5	—	1†	2·78	—	0·13†
P7	Serpentine Rivulet	20. i.55	396	9·7	6·4	23	—	1‡	4·03	—	0·03‡
P8	Serpentine Rivulet	21. i.55	444	10·2	7·0	119	3	—	14·45	0·44	—
P9	Unnamed Creek	21. i.55	396	6·7	6·2	76	1	1‡	11·01	0·22	0·01‡
P10	St. Patrick's River	24. i.55	330	36·5	20·3	41	5	—	6·97	0·81	—
P11	St. Patrick's River	24. i.55	252	33·1	14·4	22	4	—	4·84	2·06	—

*Blackfish. †Rainbow Trout. ‡*Galaxias* sp., weight estimated. §Not weighed.

TABLE 10

BASIC DATA FOR 1956

Section No.	Name of Stream	Date	Length of Section (ft)	Mean Width (ft)	Mean Depth (in.)	Number of Fish Taken				Weight of Fish Taken (lb)		
						Brown Trout		Eels	Other Species	Brown Trout	Eels	Other Species
						Total	Marked					
E1	Musselboro Creek	9. ii.56	154	16·7	15·9	25	9	3	—	7·84	1·00	—
E2 *R**	Musselboro Creek	2. ii.56	285	15·9	11·1	17	3	1	—	7·42	0·41	—
E3	Musselboro Creek	9. ii.56	270	16·3	9·3	27	—	—	—	5·73	—	—
E4 *R*	Burns Creek	2. ii.56	384	15·3	9·0	12	1	6	—	5·91	2·50	—
E5	Pig Run Creek	8. ii.56	333	11·7	8·8	30	—	—	—	6·86	—	—
E6	Ford River	8. ii.56	330	26·8	14·0	29	—	—	—	12·47	—	—
E7	Phillip's Creek	3. ii.56	478	6·2	6·8	5	—	4	—	2·06	0·56	—
E9 *R*	Ford River	3. ii.56	353	22·7	8·3	26	7	—	—	4·50	—	—
E10 *R*	Unnamed Creek	3. ii.56	204	8·2	7·7	14	1	—	—	2·56	—	—
E11 *R*	North Esk River	6. ii.56	412	16·3	12·8	10	1	—	—	2·50	—	—
E12	Evelyn Rivulet	6. ii.56	378	27·8	12·7	26	2	3	—	6·50	0·78	—
P1	Patersonia Rivulet	16. iii.56	373	24·9	17·2	56	—	3	—	10·41	1·31	—
P2 *R*	Patersonia Rivulet	16. iii.56	314	22·5	23·3	53	9	2	—	9·67	0·50	—
P4 *R*	Trout Creek	10. ii.56	408	12·9	8·3	44	9	2	1‡	4·00	0·39	0·02‡
P5	St. Patrick's River	19. iii.56	241	49·7	13·3	1	—	—	—	0·17‖	—	—
P6 *R*	Camden Brook	19. iii.56	255	25·7	26·2	4	1	—	—	0·52	—	—
P7 *R*	Serpentine Rivulet	20. iii.56	389	11·0	6·8	36	11	2	—	5·69	0·13	—
P8	Serpentine Rivulet	20. iii.56	402	13·0	7·4	104	2	4	2†	11·38	1·21	0·04†
P9 *R*	Unnamed Creek	15. iii.56	454	9·0	10·1	57	19	—	—	8·47	—	—
P11	St. Patrick's River	21. iii.56	240	36·1	20·1	22	—	1	—	6·95	§	—
P12	Patersonia Rivulet	12.xii.56	360	21·9	21·3	53	3	6	—	10·94	3·09	—
P13	Unnamed Creek	12.xii.56	364	5·8	6·9	49	—	—	—	6·06	—	—
P14	Unnamed Creek	13.xii.56	562	6·6	8·8	83	—	1	—	2·66	0·31	—
P15	Patersonia Rivulet	14.xii.56	207	4·9	6·5	38	—	—	—	2·39	—	—
P16	Patersonia Rivulet	14.xii.56	203	11·5	5·9	14	—	—	—	1·81	—	—
P17	Patersonia Rivulet	14.xii.56	387	13·6	9·8	43	—	2	—	6·67	1·80	—

**R*, position of release of 1000 marked fish in June, 1955. †Rainbow trout, 0+ fish, weight estimated. ‡*Galaxias* sp., weight estimated. §Not weighed. ‖Allowance for fish seen but lost.

Appendix II

The Natural Predators of Trout in Tasmania

It was stated above (Section IV) that natural mortality among the young fish was likely to be greater in the deeper and wider sections of a stream than near the headwaters. Some considerations of the reasons for this are given here. Greeley (1932) has shown that during spawning, unattached males of the same species, and males of other species, accompany spawning fish and avail themselves of opportunities of darting in and seizing ova being shed. This has been observed to occur in Tasmania. It is known from several sources that the platypus (*Ornithorhynchus anatinus* Shaw & Nodder) also causes some loss of eggs and young fish. Lord and Scott (1924) refute the claim that it eats fish but show that being well equipped for burrowing, and using this method for collecting much of its food, it could well disturb spawning redds and consume ova. Burrell (1927) states that the natural food of the platypus, in order of preference, consists of shrimps, earthworms, and insect larvae, and that it also eats tadpoles, molluscs, and water-weed. He points out that it comes to the surface to chew its food, and states in connection with one kept in captivity for a considerable period that it would not touch "river fish" even though they were "shrimp-size and served alive". On the other hand Harris (1956) states that the platypus eats small fish. It is clear from Burrell's account that it would not inhabit very small creeks where the banks could not accommodate its burrows, but it has been taken occasionally in the larger streams during electro-fishing, and it is in such places that the population of small trout has been found inadequate to maintain the existing population of older trout. It is probable, therefore, that it is responsible for some of the mortality of the eggs and that it would also eat recently hatched alevins, since these are of similar size to shrimps.

The following account, based on factual evidence relating to predation on young trout in Tasmanian waters, has been summarized from a statement prepared by Mr. H. V. Jones, Chief of Staff of the Salmon and Freshwater Fisheries Commissioners, whose observations are the result of over 30 years' association with the freshwater fisheries of the State. He lists the following mammals and birds, not necessarily in order of importance. The platypus, golden-bellied water rat (*Hydromys chrysogaster* Geoff.), blue (or white-faced) heron (*Notophoyx novae-hollandiae* Forster), black duck (*Anas superciliosa* Gmelin), silver gull (*Larus novae-hollandiae* Stephens), bittern (*Botaurus poiciloptilus* Wagler), and all species of cormorants, of which four are known to occur in Tasmania: the black (*Phalacrocorax carbo* L.), the little black (*P. sulcirostris* Lesson), the white-breasted (*P. fuscescens* Vieillot), and the little pied cormorant (*P. melanoleucus* Vieillot). All of these, in his personal experience, are known to have fed on trout at one stage or another, as noted below. Not included in his list are both species of trout and the native freshwater flathead, or sandy (also locally known as pike) (*Pseudaphritis urvillei* C. & V.) which have been referred to in the preceding pages. It is also probable that the introduced perch (*Perca fluviatilis* L.) and possibly the native blackfish (*Gadopsis marmoratus* Rich.) eat young trout.

Mr. Jones has observed platypus on spawning beds in streams and on the shores of lakes; at the Great Lake rainbow trout have been seen spawning along the shores of Swan Bay and platypus going from redd to redd disturbing them; three platypus have been observed at the same time working over spawning beds at Mountain Creek, Lake Sorell. In the hatcheries considerable damage can be done by platypus, and when captured there, they have disgorged quantities of partly eaten fish, up to 3 in. in length, of which they normally eat the head and leave the body. The reverse is the case with the water rats, which frequent the hatchery and take fish up to 5 in. in length from the ponds, eating the body and leaving the head and fins. If allowed access to the hatchery buildings they will also eat large quantities of eggs, though their chances of obtaining these in nature are considerably less.

Of the birds, Mr. Jones regards the blue heron as the worst predator where fish are concentrated, as in shallow rearing ponds, though ducks would rank high here. Of the heron he states that when killed and examined at hatcheries they are found to contain large numbers of fish up to 3 in. in length; one contained 237 trout up to $1\frac{1}{4}$ in. long. It is found on most of the rivers and around lakes and would cause its greatest damage when rivers are reduced to pools, and at such times and places where shallow conditions enable it to wade among the fish; recently many were disturbed on a visit to the Liawenee Canal when the flow was reduced and the fish concentrated in pools. The wild duck will take spawn and small fish, and has been seen on the spawning beds at the Great Lake, Lake Sorell, and Lake Leake. Ducks destroyed at the Plenty hatchery have had young fish in the gut, and on one occasion, practically cleaned out one small rearing pond containing 8000 trout fry. Seagulls destroyed at hatcheries have been found to contain fish up to $1\frac{1}{4}$ in.; and one bird had eaten over 50 young fish and also quantities of ova. The bittern, which is found around the shores of rivers and lakes, was seen to take a fish about 4 in. long on one occasion. As for cormorants, they are very troublesome at the hatcheries at times, and those shot on inland waters occasionally contained trout. Although most of this factual support for predation on trout by various species comes from the hatcheries, this is to be expected since it is there that the fish are concentrated and most easily taken, and it is also at such places that observations are most likely to be made. These notes show that the species listed will all feed on young trout.

THE DEVELOPMENT AND SETTLING OF A SERPULID WORM, *HYDROIDES NORVEGICA* GUNNERUS (POLYCHAETA)

By B. Wisely*

[*Manuscript received February* 13, 1958]

Summary

Hydroides norvegica larvae were reared to settling in 8–10 days at 20°C. The paired conical processes on the collar setae characteristic of the genera *Hydroides* and *Serpula* were developed in the larvae by the sixth day. Settling differed from that recorded for other larvae in that (i) larvae could become attached to surfaces comparatively early in their free-swimming life, (ii) "searching" behaviour followed by settling on a particular locus was not observed, (iii) feeding continued through metamorphosis. The primary operculum of the young worm was formed by modification of the third branchial filament of the left side. Certain identification as *H. norvegica* could not be made until this had been shed and replaced by a secondary operculum developed from the right side 4–8 weeks after metamorphosis.

I. Introduction

Hydroides norvegica (Plate 1, Fig. 1) is widely distributed throughout the world (Fauvel 1932; Hutchins 1952) and is regarded as an important fouling organism in eastern Australian ports (Allen and Wood 1950; Allen 1953) because it forms heavy encrustations on ships' hulls (Plate 1, Fig. 2) and powerhouse conduit walls. Since these encrustations are the result of successful larval settlement, which an effective antifouling surface should be designed to prevent, it seems pertinent to record some laboratory observations on the development, settling, and metamorphosis of this species.

II. Methods

Adults were scraped off docked ships' hulls in Sydney Harbour (Port Jackson) and transported without sea-water to the laboratory where they were thoroughly washed to remove injured animals and other contaminants. They were then spread out in a layer 1 in. deep in a shallow concrete tank provided with running sea-water and turned and rewashed periodically for the first few days. With this treatment eggs and sperm suitable for artificial fertilization were available for several months. All sea-water used in fertilization and rearing was passed through a "Reilax" industrial filter fitted with Hortmann-Ekwip "D9" filter pads to reduce bacteria before use. When the worm tubes were broken open into a shallow dish of sea-water ripe males and females began to discharge gonadial products from their abdominal pores, or the ruptured surfaces of their posterior segments. The latter were whitish in the males and pink in the females. These ripe adults were picked out from the rest and placed in a second shallow dish of sea-water to spawn into the relatively clean sea-water about them. It seems likely that ciliates were in some

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cases transferred with the adults at this stage and thereby introduced into the cultures. The eggs were then pipetted from this second dish into 800-ml beakers of sea-water and the sperm from several males added to each beaker. After the eggs had sunk to the bottom (about 2 hours) the supernatant sea-water was carefully poured off, disposing of much of the unused sperm, broken eggs, etc. The beakers were refilled with sea-water and left overnight. By next morning the young trochophores had left the bottom and dispersed fairly evenly through the sea-water. They were then decanted off to separate them from unfertilized or abnormally developing eggs on the bottom and put into a sintered glass filter, of 15–40 μ pore diameter, which held them back. About nine-tenths of the sea-water was allowed to pass through the filter so that most of the soluble decomposition products were removed.

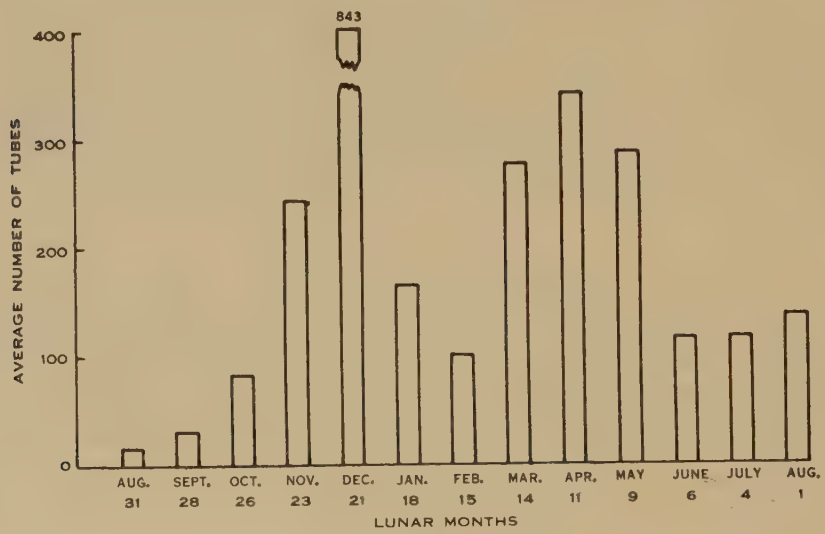

Fig. 1.—Average *Hydroides* settlement at Garden Island during 2½ years (3.viii.55–15.i.58). Based on counts of ¼ area of 14 by 9 in. roughened black bakelite plates (from C.S.I.R.O. fouling investigation files).

The larvae were then replaced in the beakers which were filled with sea-water. Then, small quantities of cultures of the small flagellate *Dunaliella terteolecta* Butcher were added. This organism, which was suggested and initially supplied by Dr. H. W. Harvey of the Marine Laboratory, Plymouth, had a width of approximately 3–6 μ and a length of 9–12 μ. It was grown in 75 per cent. sea-water enriched with Miquel's solution (Allen and Nelson 1910) and earth extract at about 28°C, using standard bacteriological techniques, and it remained freely suspended in 2½-l. cultures for over 5 months without subculturing. The density of these cultures was about $1 \cdot 7 \times 10^6$ single free cells per ml, with a chlorophyll *a* concentration of approximately 2·4 mg/l. Concentrations greater than one part of culture in eight of sea-water were avoided since in the early experiments such concentrations were accompanied by heavy larval mortality. Later work suggests that this is not as critical as first supposed, but the matter has not been closely investigated. In some cases ciliates were present

and competed with the larvae for food. The amounts of *Dunaliella* and sea-water were increased (maintaining the less than 1 : 8 ratio) until the larvae had settled, the ciliates were removed by gently flushing out the cultures overnight with running filtered sea-water, and more *Dunaliella* was added. Under these conditions development was rapid, a settling peak usually appearing in 8–10 days at an average water temperature of 20°C.

Drawings were made with the aid of phase contrast and a squared eyepiece. Some need special mention: Figures 2–8 and 15 were made of material slightly flattened under a coverslip, which produced some distortion of the trochophore stages. When free-swimming the young trochophore (Fig. 7) is distinctly lenticular in lateral view and in the older trochophore (Fig. 8) the hyposphere is narrower than is shown. The relatively bulky post-prototroch region of the fully developed larva (Fig. 9) was due to distension of the alimentary canal with *Dunaliella*, and not to flattening.

III. Developmental Observations

(*a*) *Seasonal Settling Activity*

Data obtained by immersing plates at Garden Island (Sydney Harbour) and counting the numbers of *Hydroides* tubes appearing per month are shown in Figure 1. *Hydroides* settled during each month of the year but was more prevalent during the summer and autumn (December to May). Peaks of settling activity were indicated in December and in April.

(*b*) *Fertilization and Cleavage*

The eggs appeared pink by reflected light and were opaque and spherical. Each egg (Fig. 2) was enclosed in a membrane 2 μ thick, the total diameter approximating 50 μ. Two polar bodies were extruded prior to or during the first division; in the latter case they usually lay at one end of the first cleavage furrow. A typical sperm had the outline shown in Figure 2, the head and middle piece measuring about 3·8 μ and the tail 43–47 μ. At 20°C the majority of eggs reached the two-cell stage (Fig. 3) in an hour and the four-cell stage (Fig. 4) in 1–2 hours. At the eight-cell stage the upper tier of cells had rotated 45° from the lower (Fig. 5). All blastomeres were nearly the same size, obvious differences not becoming apparent until the fourth or fifth division. Ciliated larvae with a prototroch consisting of a single ring of cilia (Fig. 6) first began to appear in 4–5 hours; these were circular when seen from above but distinctly lenticular when seen from the side.

(*c*) *The Trochophore*

A typical trochophore larva (Fig. 7) developed in 10–14 hours and consisted of a hemispherical episphere (*ep*) and a tapered hyposphere (*hy*), the two being separated by the prototroch (*pt*). An apical tuft (*at*) of several cilia was present as well as feeding cilia (Fig. 8, *fc*), a metatroch (*mt*), and a neurotroch (*nt*). The feeding cilia extended in a band around the larva and beat towards the mouth, the metatroch was post-oral in position and the neurotroch extended ventrally towards the posterior end. The cells underlying the apical tuft and the prototroch were larger than any

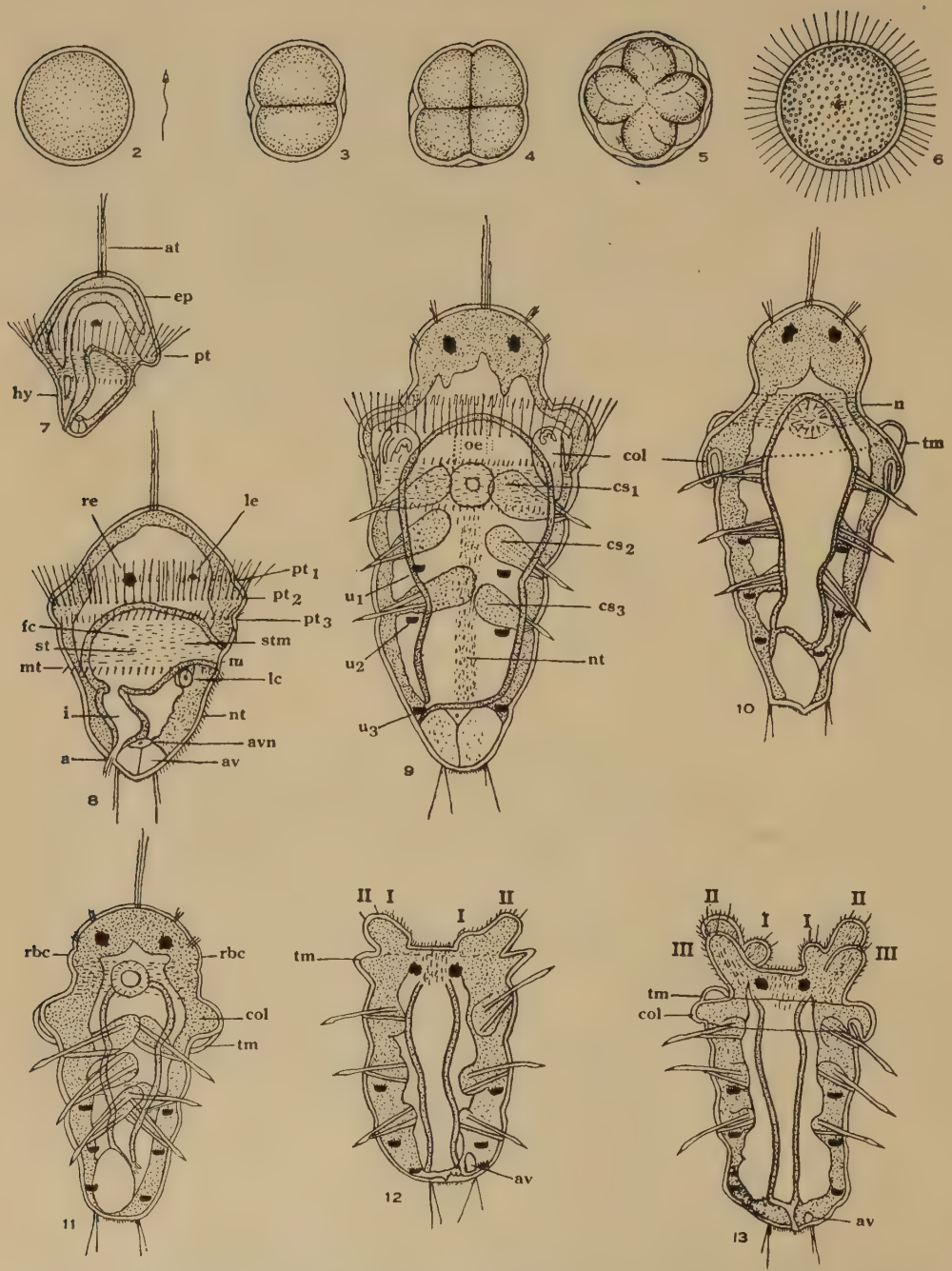

Fig. 2.—*H. norvegica* egg of approximately 50 μ diameter, and sperm. Fig. 3.—2-cell stage. Fig. 4.—4-cell stage. Fig. 5.—8-cell stage. Fig. 6.—Apical view, young trochophore, showing prototroch. Fig. 7.—Lateral view, young trochophore, slightly flattened. Fig. 8.—Lateral view, older trochophore, slightly flattened. Fig. 9.—Fully developed larva, dorsal view. Fig. 10.—Larva in early metamorphosis, dorsal view. Fig. 11.—Later stage, ventral view. Figs. 12 and 13.—Ventral views showing development of branchial rudiments. For lettering see text; all figures to same scale.

other cells present. The mouth (*m*) was followed by a short stomodaeum (*stm*) that dilated into a large stomach (*st*) and narrowed later into an intestine (*i*). A tuft of cilia projected from alongside the anus (*a*), which lay dorsally; the anal vesicle (*av*) had a prominent nucleus (*avn*) and was usually traversed by one or two threadlike structures. At this stage only the right eyespot (*re*) was present.

Provided ample food was available the trochophore increased in size rapidly during the next two days, its total length approaching 210 μ and its maximum breadth 165 μ (Fig. 8). Accurate measurements were difficult to take because of the speed at which the larvae moved, and the distortions produced when they were anaesthetized or flattened. Moreover, size was found to vary with the batch and the amount of food available. Consequently all measurements of these and later stages are only approximate (and not definitive).

Notable changes at this stage included the addition of the left eyespot (*le*) and the differentiation of the prototroch into three rings, viz. (1) a ring of short cilia anteriorly (pt_1), (2) a ring of long (the original) cilia on the equator of the prototroch region (pt_2), and (3) a ring of short cilia in the depression between the prototroch region and the prospective first setigerous segment (pt_3). One, or possibly two, very large cells (*lc*) appeared by the stomodaeum, corresponding in size and position with those of *Psygmobranchus* (Meyer 1888) and *Pomatoceros* (Segrove 1941), which the latter author considers may be the nephridial rudiments. The protonephridia did not appear to lie diagonally across the body as in *Pomatoceros* but along the intestine wall. In moribund specimens in which the short intestinal cilia had ceased beating, flame cell ciliary movement was observed in this region and was similar to that of the nephridia in the collar region of metamorphosing larvae. In this material a head vesicle was not observed.

The fully developed larva (Fig. 9) became apparent in under 6 days; its movements were more sluggish than those of the earlier stages. The head became spatulate and cilia appeared on each side of the head in the vicinity of the eyes. Considerable differentiation and increase of length had occurred in the trunk region. Three setigerous segments appeared simultaneously, each of which possessed a pair of chaetal sacs (cs_{1-3}). Each sac had two setae, the larger ones of the first pair already bearing the conical processes characteristic of the genera *Hydroides* and *Serpula*. Uncini (u_{1-3}) were absent behind the first pair of chaetal sacs but were present between the second and third. At the posterior end there was a pair of uncini which did not appear to be accompanied by setae; they lay laterally to the anterior boundary of the anal vesicle. Larval nephridia could be seen in moribund larvae; they consisted of a prominent cell on each side of the oesophagus (*oe*) from which a clump of cilia extended to near the anterior wall of the collar (*col*). Development of the latter was similar to that of *Pomatoceros* (Segrove 1941).

(*d*) *Light Reactions*

Daily observations were made on the reactions of several batches of larvae to natural light, and strong artificial light supplied by a Leitz microscope lamp. Young trochophores (24 hours from fertilization) did not show a positively phototrophic reaction to either of these sources but remained evenly dispersed in the

containers even though the right eyespot (Fig. 7) was already present at this stage. This was in contrast to first stage barnacle nauplii and certain bryozoan and tube-worm larvae where a light beam can be used initially to concentrate them. No change was noted in *Hydroides* until the fourth or fifth day when the larger trochophores of the batches (i.e. just prior to Fig. 9) showed a slight tendency to concentrate in the beam of the microscope lamp and make their way to the side of the container nearest the source. Beakers containing abnormally heavy densities of larvae (approx. 200 per ml) showed a rather similar effect when placed against a window. The larger trochophores concentrated in a band at waterline on the window side of the beakers, and near the bottom of the opposite side of the beakers. Unusually bright concentrations of light appeared to be produced at these locations by the optical properties of the beakers of sea-water. At the usual densities used here (approx. 20 per ml) the effect was still seen with a hand lens. In the next day or so the fully developed larvae (Fig. 9) became most noticeable near the bottoms of the containers and, in the main, remained there until settling. Zeleny (1905) mentions the formation of bands of larvae just below waterline on the lighted side of containers of *H. dianthus*, as also does Segrove (1941) for *Pomatoceros triqueter*, but neither records the stage of larval development, nor the condition of the cultures. According to Føyn and Gjøen (1954) this indicates unhealthy conditions in the cultures in *P. triqueter*; in healthy cultures most of their larvae settled on the bottom of the containers. In healthy cultures of *H. norvegica* the majority of larvae settled on the bottom, a small number settled just below waterline on the lighted side, and a few settled at random over the rest of the surface.

(*e*) *Settling*

The settling and metamorphosis of *H. norvegica*, as observed here, differed from that of certain other marine invertebrate larvae. In the bryozoans *Bugula neritina* L. and *Watersipora cucullata* (Busk), both of which have been observed in this laboratory, and in the serpulid *Spirorbis borealis* Daudin (Knight-Jones 1951), the oyster *Ostrea edulis* L. (Cole and Knight-Jones 1939), and commonly in barnacles, the free-swimming period is followed by one in which the larva crawls over the substratum, apparently seeking a suitable settling site. Crawling just prior to settling is characterized by its relative slowness and by sharp changes of direction so that the larva finally moves around close to the prospective settling site. With experience it is possible to recognize by their behaviour and movements when these larvae are about to settle.

Settling appeared to be much more variable in *Hydroides*. Before the larvae had reached the fully developed stage shown in Figure 9 they were beginning to secrete an adhesive substance that trailed from the posterior end of their bodies. Larvae were seen towing small pieces of bacterial film, detritus, or even smaller larvae through the cultures, often some distance behind. The presence of this "towline" could usually be demonstrated by passing a needle just behind a travelling larva; once contact was made with this substance the movements of the larva followed those of the needle. If the needle was then held stationary the larva slowly moved away from it, often to many times its length, and then accelerated to its normal travelling

speed when the connection was broken. Knight-Jones (1951) has noticed a very similar phenomenon in settling *Spirorbis* larvae. When the side of a needle was forcibly pushed against the posterior half of a *Hydroides* larva the latter adhered and rarely succeeded in freeing itself. Larvae which had adhered to large pieces of bacterial film that were too bulky for them to tow, or to the sides of the containers, were kept under observation. Feeding did not appear to be adversely affected since the stomach contents of these larvae were not appreciably different from those of free-swimming larvae in the vicinity. Complete metamorphosis followed by tube formation was observed several times. The evidence suggests that larvae may become attached relatively early in development without adverse effects.

However, the main peaks of settling in the cultures were somewhat different from this. The tendency of fully developed larvae to remain near the bottoms of the containers from the sixth or seventh day, despite attempts to attract them with a strong light beam, has already been noted. By this time the bottoms of the containers were covered with a layer of pieces of bacterial film, aggregates of *Dunaliella* and fibres. The larvae became more sluggish in their movements and glided slowly over and through this layer. In doing so many became attached by their posterior ends and others swam into openings in clumps of detritus and became held there. No evidence of pre-settling "searching" was seen; the larvae settled apparently at random amongst the detritus. Larvae which had attached to glass slides left on the bottom of the containers were treated with Leishman's stain (Gurr 1953, p. 269) and were found to be attached by strands that stained red, suggesting that the adhesive substance was a mucin.

(*f*) *Metamorphosis*

During this process a marked constriction appeared between the head and collar so that a "neck" (Fig. 10, *n*) was formed. As the proto- and metatrochs began to regress, the collar (*col*) and thoracic membrane (*tm*) became exposed as flaps at the side of the body. Larval tissue did not appear to be cast off as in *Branchiomma* (Wilson 1936) and then eaten as in *Owenia* (Wilson 1932). The larva became smaller and a reduction of the ciliary current occurred but feeding did not cease completely. The head retracted towards the collar region, and in some cases the anterior end became slightly pointed and snoutlike, resembling the snout of *Branchiomma* or the "proboscis" of *Filograna* (Faulkner 1930) and *Psygmobranchus* (Meyer 1888). Although this stage (Fig. 11) corresponded to the "creeping" stage of *Pomatoceros* it has not been observed moving great distances before settling; nor did it show pre-settling "searching" behaviour as seen in the larvae mentioned earlier. It rarely moved backwards and forwards more than a few millimetres, and then very slowly. The rudiments of the branchial crown (Fig. 11, *rbc*) appeared and differentiated (Fig. 13) into three protuberances which were ciliated and bore two to three longer cilia apically. The eyes then moved posteriorly until they lay at the level of the mouth and short cilia appeared on the ectoderm between them; these beat anteriorly. The anal vesicle began to disappear and the anus shifted from a dorsal to a more terminal position. Attachment and tube formation appeared to be by the secretion already mentioned and was at first insecure; larvae could be moved by squirting water

from a pipette but could reattach later. Some time later a tube was formed which was longer than the larva and open at both ends; calcareous spicules began to appear in the newer parts of this tube after 3–4 days.

(g) *Systematics*

The fully developed larvae (Fig. 9) bear conical processes on the first setae, a characteristic of both the genera *Hydroides* and *Serpula*; but exact identification was not possible until long after a settled larva had metamorphosed into a young

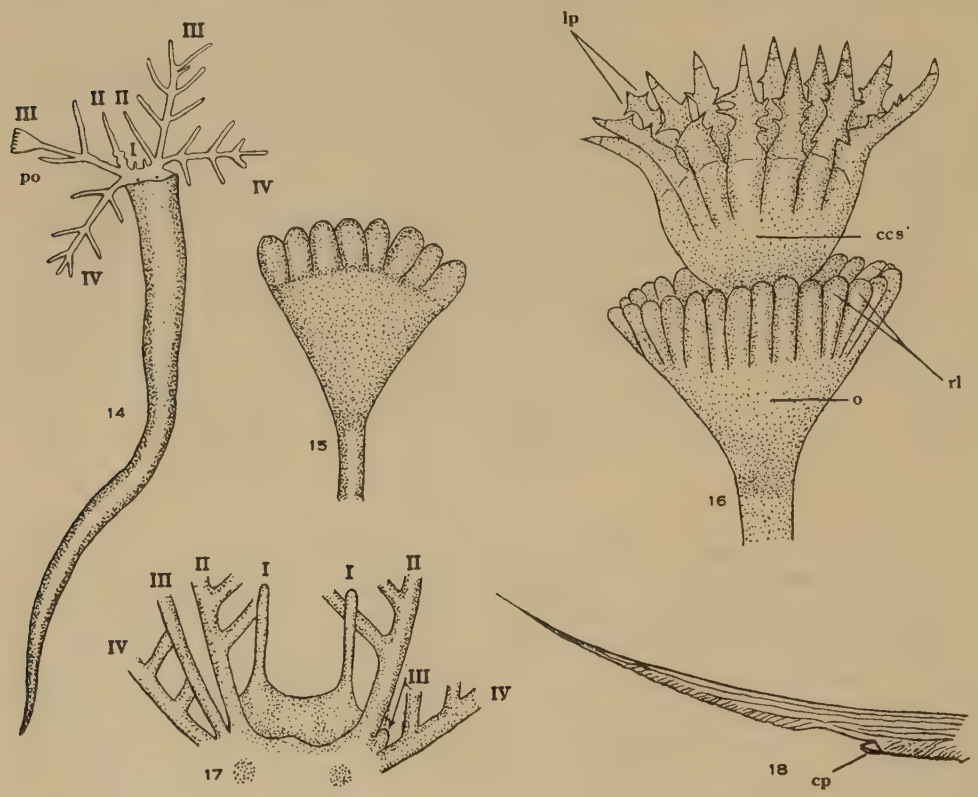

Fig. 14.—Young worm (3·0 mm tube length) showing primary operculum, dorsal view. Fig. 15.—Fully developed primary operculum developed on left side (flattened). Fig. 16.—Mature operculum. Fig. 17.—Dorsal view, branchial bases, older worm. Fig. 18.—Blade of collar seta (adult) showing conical processes. For lettering see text.

worm. The following outline of the taxonomic characters of *H. norvegica* is included here so that reference may be made to each character as it appears in development.

According to Fauvel's (1932) systematic description, the genus *Hydroides* differs from other serpulid genera in possessing a combination of (1) two conical processes (Fig. 18, *cp*) at the base of each of the collar setae blades and (2) a funnel-shaped operculum (Fig. 16, *o*) bearing a central crown of spines (*ccs*). At the specific level the number and shape of these spines and the shape of the edge of the operculum

are diagnostic; in *H. norvegica* all the spines are similar, their ends are sharply pointed and they bear several pairs of lateral processes (Fig. 16, *lp*). The radii of the operculum form rounded lobes (Fig. 16, *rl*) on the edge of the funnel. Fauvel considers that *Eupomatus elegans* Haswell 1883 (described as a new species from Port Jackson, Australia) and *H. multispinosa* Marenzeller 1884 (used by Allen and Wood (1950) but referred to subsequently by Allen (1953) as *H. norvegica*) are both synonymous with *H. norvegica*. However, Haswell (1885) in elaborating his previous (1883) description mentioned that "in the centre of the cavity of the distal segment of the operculum is frequently a strong spine like the teeth of the distal circlet and armed with spinules". Fauvel does not mention this. In a few of the specimens examined for the present paper a small dome or spine was present in the centre of the crown of spines but "spinules" were not observed. Since the appearance of this central spine was not consistent, whereas the specific characters given above were present in all mature opercula examined, Fauvel's synonymy appears valid.

(*h*) *Development of the Branchiae and Opercula*

The young worm now passes through a series of stages superficially resembling a number of other serpulid genera. The description which follows is based mainly on observations of 28 individuals which were observed from settling to the development of the secondary operculum.

When the newly metamorphosed worm protrudes its branchial rudiments from the mouth of the developing tube it is actually lying with its dorsal surface pressed against the substratum, as also occurs in *Pomatoceros* (Segrove 1941). Three pairs of branchial rudiments appear almost simultaneously. The first pair, Branchia I (Fig. 13, I), remain small, do not develop secondary branches (pinnules), and because they lie partly within the tube are difficult to observe in older worms. The second pair (II) stretch anteriorly parallel to the sides of the tube and develop pinnules. The third pair (III) at first develop pinnules but later a primary operculum develops distally on the morphological left of the pair (Fig. 14, *po*). By this time a fourth pair (IV) has been added posteriorly; other pairs appear in succession later. The primary operculum persists as a simple funnel (Fig. 15) but loses the pinnules on its stalk. Its partner branch on the right drops off and is replaced by a small bud, the secondary operculum rudiment (Fig. 17), which develops (either before or after the primary operculum is shed) into an operculum bearing the crown of spines characteristic of *H. norvegica* (Fig. 16). For some time the basal part of this operculum, viz. the funnel or primary cup, remains small; later it reaches the mature size.

This sequence is similar to that of *H. dianthus* (Zeleny 1905). In both, the newly metamorphosed worm has at first an unmodified branchia as in *Protula*, then a stage with a terminal enlargement of an otherwise unmodified branchia (like *Filograna* or *Apomatus*) followed by one in which the pinnules disappear from the stalk and the operculum bears a single row of lobes (as in *Serpula*). However, Zeleny wrote, "branchia I for the first time shows a trace of branching, seven little branchlets (pinnules) appearing simultaneously". It would appear that his "branchia I" is really branchia II, since in *H. norvegica* (and *Pomatoceros*) branchia I does not

develop pinnules, remains small, and becomes hidden from view by the tube as branchia IV appears. Branchia I is still present in older *H. norvegica* (Fig. 17) where it appears to function as a palp. Ichikawa and Takagaki (1942) have adopted Zeleny's enumeration for *H. ozoensis* but do not appear to have examined the development, without which interpretation of the older worm is difficult.

No further reversal has been observed in *H. norvegica* during laboratory development, possibly because the material was not kept long enough. As in *H. dianthus* and *H. ozoensis*, adult material taken from the sea has been noted with (1) functional operculum on right, rudimentary on left, (2) the reverse, and (3) functional opercula on both sides (see also Abeloos's (1952) cases). This suggests that further reversals can occur, as Ichikawa and Takagaki (1942) have clearly shown in *H. ozoensis*.

IV. Acknowledgments

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DEVELOPMENT AND SETTLING OF HYDROIDES NORVEGICA

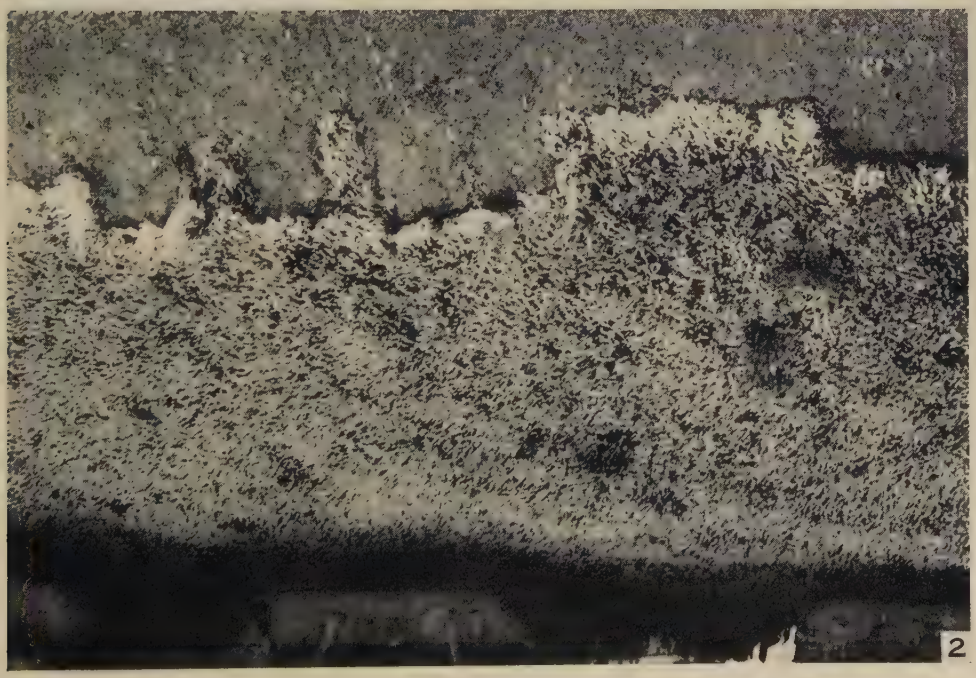

Fig. 1.—*H. norvegica* adults showing the characteristic opercula in the three central specimens. × 5.

Fig. 2.—*H. norvegica* tubes 4–6 in. long on hull of docked ship.

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THE SETTLING AND SOME EXPERIMENTAL REACTIONS OF A BRYOZOAN LARVA, *WATERSIPORA CUCULLATA* (BUSK)

By B. Wisely*

[*Manuscript received March* 31, 1958]

Summary

The external anatomy and behaviour of the pelagic, crawling, and settling stages of *Watersipora cucullata* (Busk) are described. The main settling period in Sydney Harbour appears to be February–April. The usual negatively phototropic reaction at settling in subdued light could be reversed by increasing the illumination. There was some evidence of gregariousness. When "non-filmed" settling surfaces were offered settling was delayed and a high mortality appeared. In copper solutions of 2·5–5·0 mg Cu/l. larvae settled considerably faster than the controls but metamorphosis was abnormal and lethal. No such acceleration of the settling rate was observed in mercury solutions of the same strength but these appeared to be relatively more lethal.

I. Introduction

The encrusting bryozoan *Watersipora cucullata* (Plate 1, Fig. 1) is widely distributed in tropical, subtropical, and temperate seas and has been recorded as a fouling organism in a number of these regions (Hentschel 1923; Allen and Wood 1950; Mawatari 1952*a*). In Australia it occurs in at least the eastern coast states of Queensland (St. Helena, Dunwich, Townsville) and New South Wales (Eden, Ulladulla, Jervis Bay, Port Hacking, Port Jackson, and Port Stephens). Only the Port Hacking and Port Jackson material used in the present paper has been examined for subspecific differences; it appears to fit Mawatari's (1952*a*) redescription of *Watersipora cucullata* (Busk) although the operculum (Fig. 1) is slightly different from his figure.

There are indications that the main liberation of larvae at North Head, Sydney Harbour, takes place during February and May (Fig. 2); these are late summer months when the water temperature is about 20°C. Settling does not cease during the remainder of the year. Similar results were obtained from other exposure stations in Sydney Harbour more recently but since smaller numbers of larvae had settled only the main settling peak (February–May) was detected.

Watersipora has caused concern in Australian ports, notably Sydney Harbour (Port Jackson), because of its ability to attach to moderately toxic paints on ships (Plate 1, Fig. 2). It is usually the first macroscopic form to attach in such cases and serves as an attachment surface for other less resistant fouling organisms. Weiss and Ketchum (1945) have already noted that copper paints of moderate toxicity were readily fouled by this species at Miami Beach, Florida, and at the same locality Weiss (1947) reported that its resistance to copper poisoning was higher than that of the local barnacles *Balanus amphitrite niveus* Darwin, *Balanus*

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improvisus Darwin, and *Balanus eburneus* Gould. The observation of Weiss and Ketchum (1945) that the attachment was sometimes loose on these paints has since been confirmed by Laurie (1955) for copper paints in Sydney Harbour and has also been noted subsequently on mercurial paints.

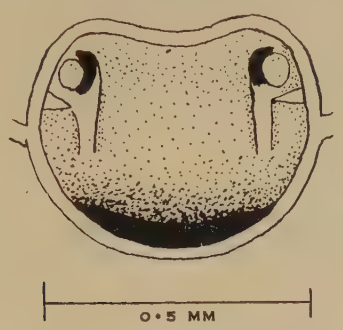


Fig. 1.—Operculum of adult material used.

II. Methods

Colonies were scraped off piles or copper sheathing in Port Hacking, thoroughly washed, and placed in concrete or Perspex tanks provided with ample running sea-water. Larvae were obtained by keeping the adults in darkness overnight

Fig. 2.—Settling of *Watersipora* at North Head, Sydney Harbour. Average monthly settlements over 5 years (1947–51) on 3 by 4 in. black bakelite plates (data from C.S.I.R.O. fouling investigation files). Water temperatures are monthly averages for 10 years in Sydney Harbour (from Fischer 1940).

and then exposing them to artificial light; the liberated larvae concentrated at the light source and were pipetted from there directly into smaller containers. Larvae used in experimental work were collected 30 min after the adults had begun to be illuminated; hence their age was 0–30 min which was small compared with their total presettlement life. Unless otherwise stated experiments were conducted in Petri dishes measuring 100×10 mm and at 19–22°C. Dishes were "filmed", i.e.

immersed in sea-water for a few days so that they acquired a film of bacteria, diatoms, or algae on which the larvae were more inclined to settle than on clean glass. However, for the tests with copper and mercury solutions only chemically clean glassware was used, since Weiss and Ketchum (1942) have shown that filmed surfaces can accumulate copper. In these tests sets of nine dishes, each containing 50 ml of solution, were placed at random in a darkened constant temperature bath at $22 \cdot 5 \pm 1$°C. Three had filtered sea-water as controls, three had copper solutions of $1 \cdot 25$, $2 \cdot 5$, and $5 \cdot 0$ mg Cu/l. in filtered sea-water, and three had mercury solutions at the same concentrations. Cupric citrate (BDH) was used as the copper source since according to Ketchum (1952) it forms a complex ion that is very soluble in sea-water and is not limited to $0 \cdot 5$ mg Cu/l. as is that of inorganic cupric salts. The mercury solutions were prepared from mercuric chloride (AR). Ten larvae were pipetted onto a small piece of glass, the excess water sucked off, and the glass immersed in the appropriate dish until the larvae swam off. This kept the amount of water low in comparison with the 50 ml of solution. The larvae were examined at 5, 15, and 25 hours after the start of the experiment.

III. Developmental Observations

(*a*) *Early Development*

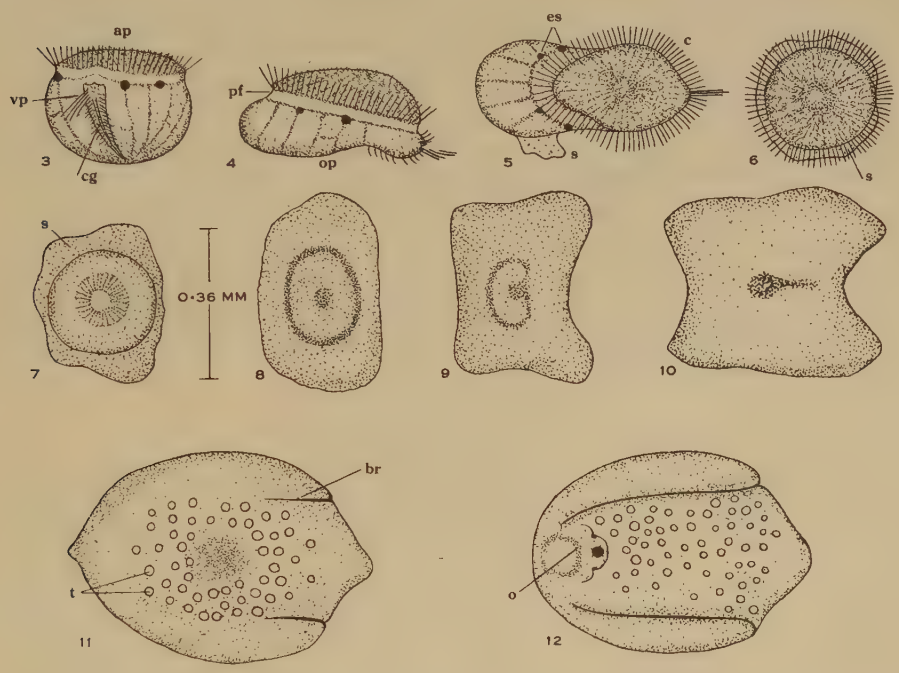
Mawatari (1952*b*) has already described the early development of *W. cucullata*, which appears, from the photographs, to be the Japanese var. *watersi* form *labiosa* he had described earlier (1952*a*). He considers it a hermaphrodite species, usually self-fertilizing, with an isolecithal egg and holoblastic cleavage to the 16-cell stage. Sperm entry may occur before maturation, fertilization is monospermic, and larval development concomitant with polypide degeneration. After liberation of the larva, which usually settles within 24 hours, a new polypide appears and a second egg begins to develop about 4–5 weeks after the polypide has become functional. Mawatari suggests that each *Watersipora* zooid is able to emit, at the most, only two or three larvae a year.

(*b*) *Larvae*

The larvae (Figs. 3, 4, and 5) are bright red, roughly spherical, and measure between $0 \cdot 34$ and $0 \cdot 40$ mm in diameter, excluding the coronary cilia; the aboral pole (*ap*, = "calotte" of Barrois (1879)) is marked with fine radiating striae and is flattened in swimming larvae; the corona (*c*) is equatorial, pigmented, and bears a ring of long cilia used in swimming; these border the pallial furrow (*pf*). The anterior of the two pairs of eyespots (*es*) is slightly larger than the other pair. The oral pole (*op*) is hemispherical in swimming larvae, and it bears a ciliated groove (*cg*) corresponding to the lateral groove of Grave (1930). The vibratile plume (*vp*) consists of about four large cilia that project from its pallial furrow end and beat in unison. For most of its length the ciliated groove is broad, shallow, and provided with lateral cilia; it terminates in a clear area from which the large internal sac (*s*) is evaginated during settling. Pigmented lines divide more particularly the posterior half of the oral pole into large irregular sections.

(c) *The Pelagic and Searching Stages*

It was observed that after liberation larvae swam towards a light source with their aboral poles anteriorly; they usually moved spirally around the longitudinal axes of their paths. The duration of the pelagic, positively phototropic, stage varied between 2–5 hours (depending partly on the illumination and availability of suitable settling surfaces) and merged into a stage where the larvae seemed "indifferent" to light; they usually left the most illuminated side of the dish and



Figs. 3–12.—Larva of *Watersipora cucullata*. Fig. 3.—Anterior view. Fig. 4.—Lateral view, crawling stage. Fig. 5.—Settling stage from above. Fig. 6.—Settled larva 25 sec later. Fig. 7.—"Umbrella" stage from above. Figs. 8–12.—Development of ancestrula (first zooid) from above. All larval stages to same scale with larval anterior end on right in Figs. 4–12. For lettering see text. (Figs. 3–6 are freehand drawings of moving specimens; the remainder were made with the the aid of a squared eyepiece and graph paper.)

swam more at random, often taking up positions just under the surface of the water where they hung from the surface film, slowly revolving. It is conceivable that if this happened in the sea, larvae could drift appreciable distances in calm conditions without expending much energy. This stage lasted 1–3 hours and was often punctuated by short excursions around the container, particularly to the bottom.

On alighting the larvae assumed a characteristic crawling shape (Figs. 4 and 5); the aboral pole became flattened, diamond-shaped, and often beaked above the vibratile plume. The oral pole containing the eversible sac became temporarily swollen at the posterior end and the larva moved slowly over the substratum,

constantly beating down on it with the vibratile plume. Movement was effected mainly by the coronary cilia. On encountering an obstacle with the vibratile plume the larva contracted to a spherical shape and then altered course at an angle to the original direction.

(*d*) *Settling*

The movements of settling larvae were observed by utilizing their preference for a filmed surface. When larvae which had been kept in a chemically clean dish for several hours were given such a coverslip a high proportion usually settled rapidly (i.e. within 3–4 min) particularly if the lighting was reduced.

The behaviour of such a larva was appreciably different from previous stages. It crawled more slowly and was more prone to show an avoiding reaction with obstacles, consequently its radius of movement was decreased. Powerful muscular contractions became evident, the larva pressing the lateral margins of its ciliated groove against the substratum. Two stages in the final settlement are shown in Figures 5 and 6. In Figure 5 a portion of the eversible sac (*s*) has begun to appear under the posterior part of a larva and in Figure 6 it has spread peripherally and the larva has contracted to a sphere. The aboral surface became depressed and darker in the centre, the brown eversible sac being firmly anchored to the substratum and functioning as a holdfast.

(*e*) *Metamorphosis*

The formation of the next or "umbrella" stage has already been described for *Flustrella hispida* (Prouho 1890) and *Bugula neritina* (Lynch 1947). According to Lynch it involves a sudden evagination of the apical epithelium bordering the pallial furrow which grows towards the substratum and eventually fuses with the holdfast. The vibratile plume and associated structures thus become enclosed within a new covering. This stage was reached in *Watersipora* 3–5 min after the initial attachment. The larva constricted at the proximal end of the extruded eversible sac and raised itself (except for the attaching surface of the holdfast) well clear of the substratum. The striated area of the aboral pole quickly decreased in diameter (Fig. 7) and moved into a shallow pit in its centre. In *Flustrella*, Prouho (1890) considered this invaginated portion, combined with an internal mesodermal rudiment, to form a meso-ectodermal disk which later gave rise to the polypide rudiment. About 5–10 min after attachment the *Watersipora* larva sank back onto the substratum. This stage was usually circular, flattened, and characterized by two concentric pigmented rings, the central one of which was later replaced by a dark spot. About an hour after attachment the larva expanded transversely to form an oblong shape whose long sides were at right angles to the longitudinal axis of the settling larva (Fig. 8). From $1\frac{1}{2}$ to 2 hours after attachment the future posterior end of the ancestrula or primary zooid broadened (Figs. 9 and 10). At 20 hours the anterior and posterior ends of the ancestrula had become pointed (Fig. 11), tremophores (*t*) had appeared, and two black ridges (*br*) had begun to appear from the posterior end. At 45 hours the operculum rudiment (Fig. 12, *o*) had begun to differentiate and during the second or third day the ancestrula began feeding.

IV. Experimental Observations

(a) *Light Reactions*

Watersipora larvae are positively phototropic when liberated, then "indifferent" (i.e. less attracted by light), and negatively phototropic immediately prior to settling, as are many other marine invertebrate larvae. This is under laboratory conditions; however, it was noted that increasing the illumination on settling larvae often resulted in their moving towards the light source, whereas if they were entirely negatively phototropic they should have moved away from it. Some experiments were carried out to ascertain how their reactions in bright light differed from those in the more subdued light of the laboratory. Larvae were pipetted into

Table 1

SETTLING OF LARVAE IN LIGHT AND DARK CONDITIONS

In 180–200 Candles/sq. ft			Duplicate Series in Total Darkness		
	Larvae Settling in			Larvae Settling in	
Expt. No.	Brighter Half of Dish (190–200 Candles/sq. ft)	Darker Half of Dish (180–190 Candles/sq. ft)	Expt. No.	One Half of Dish	Other Half
1	26	8	1	7	8
2	10	3	2	13	6
3	8	5	3	8	7
4	6	4	4	2	6
5	21	8	5	6	3
6	16	9	6	6	4
7	17	3	7	16	17
8	15	7	8	10	9
9	13	6	9	8	16
10	11	2	10	6	3
11	9	4	11	9	10
12	17	8	12	8	7

Petri dishes arranged parallel to a 40-W Osram "natural" fluorescent tube at a distance that gave a brightness, measured with a Weston exposure meter, of 200 candles/sq. ft on the near edge of the dish, 190 at the centre, and 180 at the far side. 200 candles/sq. ft was considered representative of the brightness at the surface of harbours on sunny days in this region. A duplicate series was run in total darkness to determine to what extent gregariousness was involved in those experiments.

The tendency of larvae to settle in the most illuminated (190–200 candles/sq. ft) half of the dish (Table 1) is of interest since it is the reverse of what occurs under ordinary laboratory lighting.

Since the larvae settled more or less at random on both sides of the dishes in total darkness, it is considered that gregariousness was not involved to any great extent; it should be noted, however, that there are indications of the phenomenon

when larvae are put in dishes containing previously settled larvae. This is discussed later. It has been noted that negatively phototropic behaviour usually eventuates when the larvae enter a dimly lighted area. When pieces of filmed shells, stones, or other opaque objects were added to dishes containing larvae, the latter tended to remain on the darker, underneath sides of those objects once they had found them. If the objects were overturned so that the larvae were again exposed to bright illumination they became agitated and usually swam towards the light. Many of the early attempts at observing their behaviour at the moment of settling were unsuccessful because of this reaction. It would appear that not only the brightness and duration of the illumination, but also the availability of cover needs to be taken into account in assessing the reactions of these organisms.

TABLE 2

COMPARISON OF NUMBERS OF LARVAE SETTLING IN PREVIOUSLY COLONIZED AND UNCOLONIZED HALVES OF DISHES IN TOTAL DARKNESS

Expt. No.	Number Settling in	
	Previously Colonized Half	Uncolonized Half
1	12	9
2	9	7
3	16	8
4	5	3
5	15	10
6	26	13
7	21	18
8	17	4
9	20	6
10	13	4
11	19	8
12	9	2

(*b*) *Gregariousness*

An experiment was carried out to see if there was any evidence that *Watersipora* showed gregariousness during settling, as has been reported in certain oyster, barnacle, and tubeworm larvae (Knight-Jones 1951). It is difficult to observe this amongst larvae of the same age when they are settling (Table 1, total darkness series), but if previously settled larvae are present there is a tendency to clump around these (Table 2). Ten larvae were induced to settle on the lighted sides of filmed Petri dishes, any not settling there being carefully scraped off. Larvae (9–42) were then placed in these dishes in 10 ml of sea-water 24 hours later and left for a further 20 hours in total darkness so that the newly introduced larvae would be able to settle.

It appears from Table 2 that the larvae showed a tendency to settle around previously settled larvae.

TABLE 3

CONDITION OF LARVAE IN SEA-WATER AND IN COPPER AND MERCURY SOLUTIONS AFTER 5, 15, AND 25 HOURS IMMERSION, DUPLICATE SERIES

Experiment	Total Larvae	Free-swimming	Dead before Settling	Settled	Settled but Dead or Abnormal	Meta-morphosing	Meta-morphosing Abnormally	Not Settled, Abnormal Metamorphosis
After 5 hours								
Controls (pooled)	60	58	1	—	—	1	—	—
Cu 1·25 mg/l. (1)	10	10	—	—	—	—	—	—
(2)	10	9	—	1	—	—	—	—
Cu 2·5 mg/l. (1)	10	6	1	—	3	—		—
(2)	10	1	—	—	9	—	—	—
Cu 5·0 mg/l. (1)	10	—	—	—	10	—	—	—
(2)	10	—	—	—	10	—	—	—
Hg 1·25 mg/l. (1)	10	—	4	—	6	—	—	—
(2)	10	—	5	—	5	—	—	—
Hg 2·5 mg/l. (1)	10	—	7	—	3	—	—	—
(2)	10	—	9	—	1	—	—	—
Hg 5·0 mg/l. (1)	10	—	10	—	—	—		—
(2)	10	—	7	—	3	—	—	—
After 15 hours								
Controls (pooled)	60	49	7	4	—	—	—	—
Cu 1·25 mg/l. (1)	10	4	—	—	3	—	—	3
(2)	10	1	6	1	2	—	—	—
Cu 2·5 m g/l. (1)	10	—	1	—	7	—	—	2
(2)	10	—	—	—	10	—	—	—
Cu 5·0 mg/l. (1)	10	—	—	—	10	—	—	—
(2)	10	—	—	—	10	—	—	—
Hg 1·25 mg/l. (1)	10	—	6	—	4	—	—	—
(2)	10	—	5	—	5	—	—	—
Hg 2·5 mg/l. (1)	10	—	8	—	2	—	—	—
(2)	10	—	9	—	1	—	—	—
Hg 5·0 mg/l. (1)	10	—	10	—	—	—	—	—
(2)	10	—	7	—	3	—	—	—
After 25 hours								
Controls (pooled)	60	26	19	—	—	13	—	2
Cu 1·25 mg/l. (1)	10	4	—	—	—	—	6	—
(2)	10	—	10	—	—	—	—	—
Cu 2·5 mg/l. (1)	10	—	—	—	7	—	1	2
(2)	10	—	—	—	10	—	—	—
Cu 5·0 mg/l. (1)	10	—	—	—	10	—	—	—
(2)	10	—	—	—	10	—	—	—
Hg 1·25 mg/l. (1)	10	—	6	—	4	—	—	—
(2)	10	—	5	—	5	—	—	—
Hg 2·5 mg/l. (1)	10	—	8	—	2	—	—	—
(2)	10	—	9	—	1	—	—	—
Hg 5·0 mg/l. (1)	10	—	10	—	—	—	—	—
(2)	10	—	7	—	3	—	—	—

(c) *Reactions in Copper and Mercury Solutions*

The tendency for the controls to remain free-swimming and to die (apparently through exhaustion) in chemically clean dishes is notable and similar to that recorded for *Spirorbis* by Knight-Jones (1951). *Watersipora* in filmed dishes showed 94 per cent. settlement in 20 hours (Tables 1 and 2) whereas in the chemically clean dishes used in the experiment described in Table 3, only 22 per cent. of the controls had settled in 25 hours. Larvae in the mercury series died relatively more quickly than those in the copper and control series, the majority being dead or moribund before settling. Their inclusion in the "settled but dead or abnormal" column was merely for convenience and does not indicate that there had been an acceleration of the settling rate. Such larvae invariably extruded their adhesive eversible sacs just prior to death with the result that many of them gave the false impression that they had settled there in the normal way. The beginning of metamorphosis was not observed in any of these larvae but was apparent in the copper and control series, where the attachment was also much firmer. The presence of 5·0 mg Cu/l. appeared to be associated with a marked increase in settling; all 20 larvae in this category settled and commenced metamorphosis. At this time (5 hours) 58 out of the 60 controls were still free-swimming, one had settled, and one was dead. Larvae in the more dilute copper solutions appeared to be intermediate in their reactions between the two.

V. Acknowledgments

This work forms part of a programme on the biology of fouling organisms in cooperation with the Royal Australian Navy. Thanks are due to Mr. P. Deane, R.A.N., for Plate 1, Figures 1 and 2.

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SETTLING AND REACTIONS OF WATERSIPORA CUCULLATA

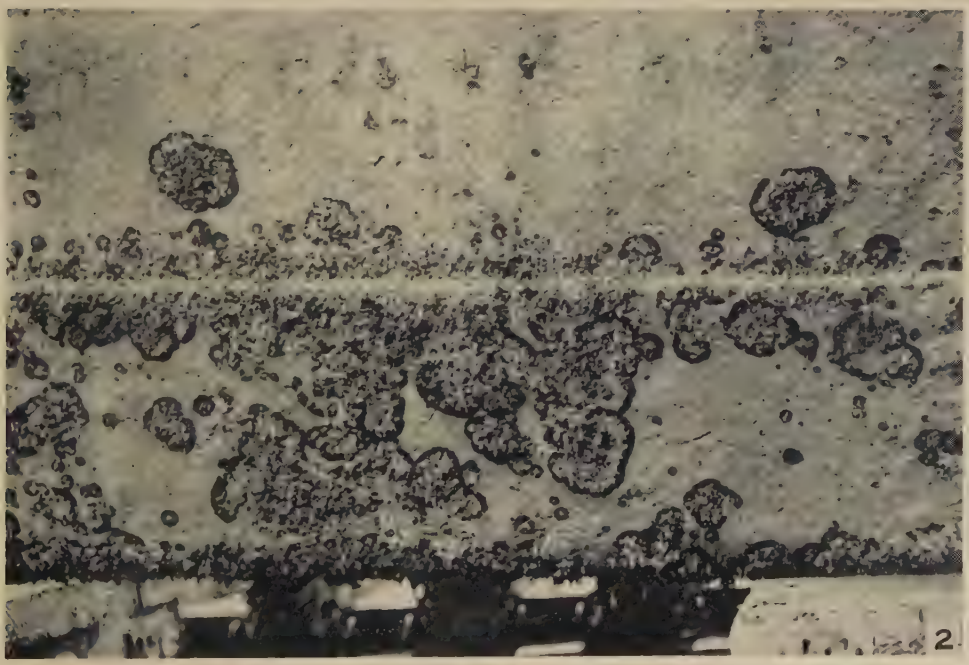

Fig. 1.—A *Watersipora cucullata* colony being used as a settling surface by other organisms.

Fig. 2.—A docked ship's hull showing colonization of an antifouling paint surface by the copper-resistant *Watersipora*, which in turn is being utilized as a settling surface by the less resistant tubeworm *Hydroides norvegica* Gunnerus.

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A MONOGRAPH OF THE FRESHWATER MUSSELS (MOLLUSCA: PELECYPODA) OF THE AUSTRALIAN REGION

By D. F. McMichael* and I. D. Hiscock†

[*Manuscript received January* 28, 1958]

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Summary

This monograph incorporates a systematic revision of the freshwater mussels of the Australian Region (Australia, New Zealand, New Guinea and the Solomon Islands). Previous systematic works are revised and discussed. Details of the taxonomic procedures used in the present work are presented. One aberrant New Guinea genus, *Haasodonta*, with two species is referred provisionally to the family Unionidae Fleming, subfamily Rectidentinae Modell. The remainder of the Australasian species are assigned to the family Mutelidae Gray. Four subfamilies, Velesunioninae Iredale, Lortiellinae Iredale, Hyridellinae Iredale, and Cucumerunioninae Iredale, are recognized. These include eight genera, *Velesunio* Iredale, *Alathyria* Iredale, *Westralunio* Iredale, *Microdontia* Tapparone Canefri, *Lortiella* Iredale, *Hyridella* Swainson, *Cucumerunio* Iredale, and *Virgus* Simpson. The genus *Hyridella* includes four subgenera, *Hyridella* s.s., *Protohyridella* Cotton & Gabriel, *Nesonaia* Haas, and a new subgenus for *H. menziesi* Gray. These eight genera include 27 species, three of which are polytypic. Three additional species are considered of doubtful validity and two nominal species are listed as *nomina dubia*. Each taxon is redescribed and all available data of shell morphology, soft anatomy, larval stages, distribution, and type material are presented. The distribution of the Australian and New Guinea species in relation to the fluvifaunal provinces of Iredale and Whitley is considered and a new name is proposed for the fluvifaunula of southern New Guinea. The evolutionary relationships of the Australasian freshwater mussels are discussed and it is suggested that, with one exception, they arose from a single ancestral stock and have subsequently differentiated into four subfamilies within this region. This view is supported by the close anatomical similarity between them.

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I. Introduction

Freshwater mussels, commonly referred to as naiades, unios, or unionids, are an abundant and widespread group of freshwater lamellibranchs of the order Eulamellibranchiata. The capacity of some of them to produce pearls has excited interest in the group since early Roman times, whilst in some regions, particularly the United States, they have formed the basis of an extensive pearl button industry. They have been used frequently as the basis for zoogeographic studies, though their value as evidence in this regard is open to question. For these reasons, they have been, in certain regions, the subject of systematic and ecological study for a long time.

In the Australian Region (or Australasia), which in this monograph is taken to include Australia, New Zealand, New Guinea, and the Solomon Islands, study of the group has lacked the stimulus of economic interest, and systematic knowledge of the group has lagged behind that of other regions. It has not been appreciated, previously, that the freshwater mussels of the Australian Region, with one exception, form an indivisible unit, separate and distinct from the neighbouring Indo-Malayan fauna. Previous workers have tended to study the mussel faunas of the constituent islands of the Australian Region as unrelated units, though relationships have been suggested, notably by Simpson (1896), and in some cases established, by Haas (1924) and Dell (1953), but never in a comprehensive manner.

Early records of freshwater mussels from Australasia appeared in the works of European and American malacologists. Much of this material was collected by naturalists and explorers in Australia, and lacked adequate data. This was due, partly, to the poorly known geography of the continent at the time and also to the lack of appreciation of the value of exact geographic information.

Smith (1881) provided the first critical survey of Australian mussels, in which he listed and critically reviewed the described species. His work stood for many years but it has since proved incorrect in many nomenclatural details; all species but one were assigned to the genus *Unio*, the genus to which most had been assigned by their original authors. Simpson (1900, 1914) was the first to separate the majority of the Australasian species from *Unio*, recognizing their similarity to the South American species of the genus *Diplodon* Spix. He allotted most of the Australian and New Zealand species to *Diplodon*, with *Hyridella* Swainson used subgenerically. Despite his earlier (1896) observations of the probable relations of Australian and New Guinea mussels, he placed the New Guinea species in very different groups.

Significant observations on Australian mussels were made by Frierson (1908) and Ortmann (1912, 1920*a*), while Haas (1924) correctly related some New Guinea species to those of Australia.

The first comprehensive review of the group by Australian workers was made by Cotton and Gabriel (1932). Their work included Australian species only and, though marred by poor nomenclature, recognized the important differences in beak sculpture amongst the major groups of Australian mussels.

Iredale (1934, 1943*a*, 1943*b*) reviewed the Australian species, making a significant contribution from the nomenclatural point of view and recognizing the several groups of mussels comprising this fauna. In detail his results were unsatisfactory; his

assignment of names was often incorrect, his excessive splitting made the recognition of species difficult and obscured generic relationships, and he did not consider any New Zealand or New Guinea species, nor any extralimital forms, with the resulting creation of an unnecessary family name.

Recently Dell (1953) reviewed the New Zealand freshwater mussels and his studies have assisted materially in the present work. In applying modern systematic concepts to this group, Dell has made a significant contribution to freshwater mussel taxonomy.

Finally a review of New Guinea mussels has been published recently (McMichael 1956) and the fossil species also have been reviewed (McMichael 1957).

Almost without exception, the studies prior to that of Dell (1953) have suffered from two serious shortcomings: (i) Many early descriptions of species were so brief and undetailed that, even when accompanied by illustrations, accurate recognition of the species was difficult. The obvious solution to such a problem is recourse to type material, yet with one partial exception (Simpson 1900, 1914), this had not been done. In the present work, one of us (D.F.M.) has been able to examine most of the existing type material, much of which is housed in overseas institutions. This has rendered specific identification much more accurate and has revealed numerous mis-assignments in previous works. (ii) It has become quite obvious, during the present work, that in many cases individual freshwater mussel shells are inadequate for critical taxonomy. The vicissitudes of the environment over large areas, particularly in Australia, lead to immense variability in shell shape within a single species. Only by studying large populations of mussels from as wide a range as possible is the taxonomist able to recognize differences at specific, subspecific, and population ecotype level. Many early descriptions were based on a single shell or at best a small series from a single locality. Consequently, many of these "species", though quite different in appearance, have proved to be no more than ecophenotypes from different localities within the range of a single species. The delimitation of a species, or the "species concept", as understood in the present work, will be discussed in detail below.

The taxonomic procedure used in the present work, while not entirely original or novel, is based upon an assessment of the value of morphological, embryological, and cytological characters useful in taxonomic discrimination. Before presenting an account of the taxonomy of the Australian species, some remarks on procedure and taxonomic characters are therefore necessary.

II. Taxonomic Procedure

(a) *Taxonomic Characters*

(i) *Shell Morphology.*—The shell of a freshwater mussel generally consists of two equal valves exhibiting a variety of structural details which are of importance as taxonomic characters. Figure 1 shows the terminology of some of these characters.

(1) *Size.*—The Australasian species range in adult size from about 40 mm in length to about 200 mm. Absolute length is not, in itself, generally a useful taxonomic character. In some cases, sufficient material has been examined to allow a maximum

length limit to be stated for a particular species, and when a specimen in question is known to be fully adult, its size may assist in its identification. Absolute measurements of various other dimensions of a shell are similarly of little use, but relative dimensions which partly express shell shape are of fundamental importance.

(2) *Shape.*—The particular shape of the mussel shells is frequently difficult to express in quantitative terms. Certain obvious dimensions such as total length, maximum height, and maximum width are often measured, but these alone are not discriminating. Several systems of measuring shells have been used in attempts to overcome this difficulty, but none of them is completely satisfactory. While measurements of angular dimensions would be most useful, they are wholly impracticable, the main difficulty lying in standardizing base lines which are necessarily tangential

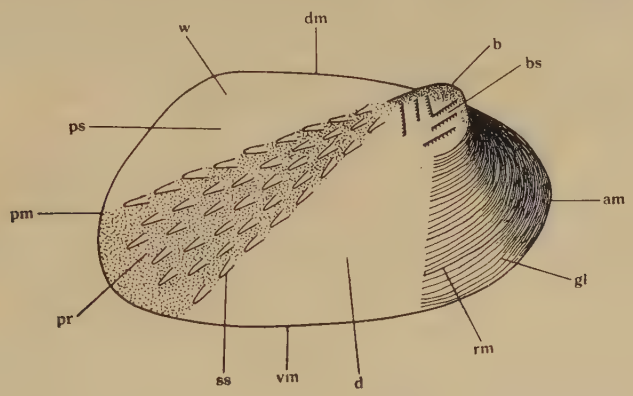

Fig. 1.—Diagram of external shell characters on the right valve of a hypothetical freshwater mussel. *am*, anterior margin; *b*, beak; *bs*, beak sculpture; *d*, disk; *dm*, dorsal margin; *gl*, growth lines; *pm*, posterior margin; *pr*, posterior ridge; *ps*, posterior slope; *rm*, rest marks; *ss*, shell sculpture; *vm*, ventral margin; *w*, wing.

to curved surfaces. Among the more comprehensive systems proposed, that of Agrell (1949) and that of Dell (1953) give good results. The system used here is a modification of these; Figure 2 shows the dimensions used. A single left valve is orientated on a metric grid to cover its maximum length. Maximum height is measured at right angles to this plane. Beak height is measured on the inside of the valve and is the height of the shell from dorsal to ventral margins at the position of the beak, excluding the height of the beak itself above the hinge-line. Maximum width is measured on the complete shell with calipers. All measurements are taken to the nearest millimetre.

Three indices are calculated from the absolute dimensions. The beak length relative to maximum length is termed the Beak Length Index (BLI), the maximum height relative to maximum length is termed the Maximum Height Index (MHI), and the beak height relative to maximum height is termed the Beak Height Index (BHI). These three indices, which are expressed as percentages, prove most useful in characterizing, in quantitative terms, the general shape of a shell and the range of variation in shape within a given species.

(3) *Hinge and hinge teeth.*—The hinge of freshwater mussels shows considerable variation throughout the group and is frequently of key importance in species differentiation. Modell (1942) considers that the primitive hinge in this group possessed lamellar teeth only, with two short cardinal teeth and two longer lateral teeth in the left valve and a single cardinal and lateral in the right. Subsequently, the hinge-line became arched dorsally and the cardinal teeth were modified by splitting up to become stronger, more compact, and complexly grooved. The primitive hinge type can be referred to as "lamellar" while the later modification can be referred to as "unionid". In other regions of the world, there has been further development, leading to the more complex hinges of the North American Quadrulinae and the secondarily taxodont hinge of the African genus *Iridina*. Figure 3 illustrates these developments. In the Australasian species, the hinge structure varies from simple lamellar to complex unionid, with a few cases of almost total reduction of teeth.

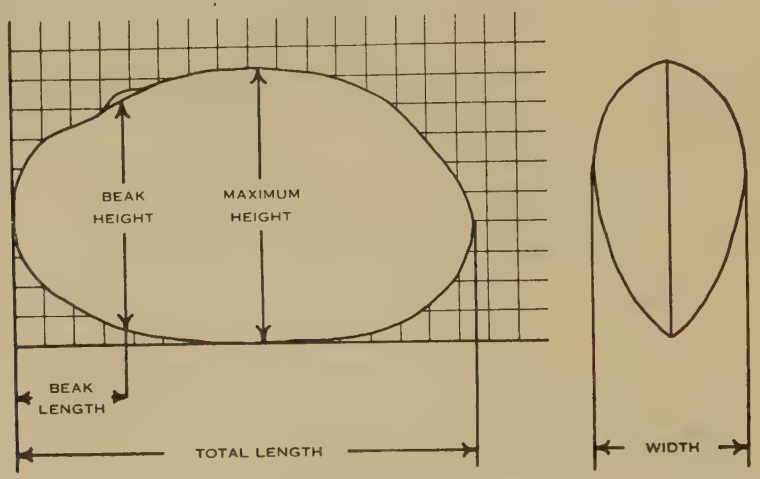

Fig. 2.—Scheme for measuring dimensions on mussel shells. A metric grid, ruled in mm, is used for dimensions other than width.

(4) *Muscle scars.*—The position and nature of the four groups of muscle scars are illustrated in Figure 4. Only the scars of the adductors and their associated muscles are of much taxonomic use and the anterior set are the more important. Most species show little variation in their arrangement.

(5) *External sculpture.*—This falls generally into two divisions: beak sculpture and the sculpture of the remainder of the shell surface. Though the former may have given rise to the latter, both phylogenetically and ontogenetically, the two are best considered separately. Neither of these developments should be confused with the concentric growth lines which are always present in the shell (see Fig. 1).

Shell surface sculpture is generally constant for the species and takes the form of pustulose nodules and folds, usually arranged in definite patterns on definite portions of the surface. The nodules are often fused to form ridges. Overall sculpture pattern is generally constant for a genus, varying in degree of development and in position in different species.

Beak sculpture is of key taxonomic importance: it usually takes the form of small ridges which develop on the valves of the very young shell and are retained in the adult, confined to the beaks. Sometimes the ridges are continuous with the

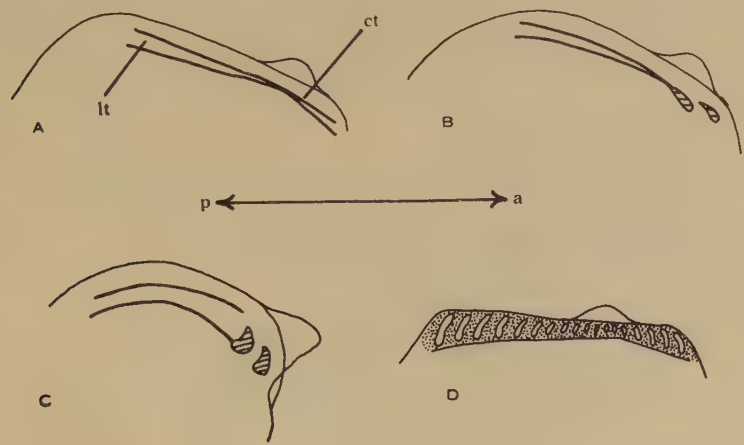

Fig. 3.—Hinge development in freshwater mussels. *A*, lamellar; *B*, unionid; *C*, quadrulid; *D*, secondarily taxodont hinge of *Iridina*. *a*, anterior end; *p*, posterior end; *ct*, cardinal teeth; *lt*, lateral teeth.

shell surface sculpture. Since the beaks are frequently eroded and corroded, beak sculpture is impossible to determine in many adult shells. Most Australasian mussels lack beak sculpture and must be regarded as more primitive than those possessing

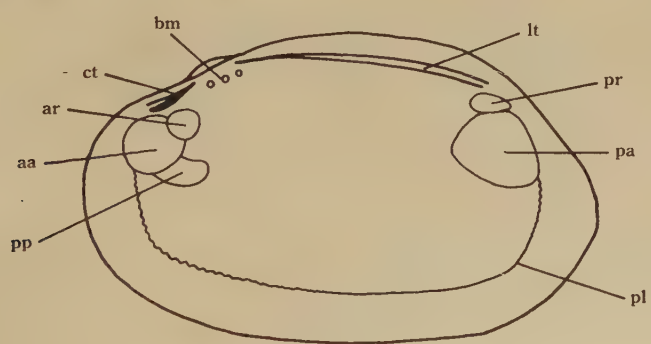

Fig. 4.—Internal shell characters of a freshwater mussel. *aa*, anterior adductor muscle scar; *ar*, anterior retractor muscle scar; *bm*, beak muscle scars; *ct*, cardinal tooth; *lt*, lateral tooth; *pa*, posterior adductor muscle scar; *pl*, pallial line; *pp*, pedal protractor muscle scar; *pr*, posterior retractor muscle scar.

it, since the earliest (Triassic) fossil mussels from Australia seem to lack sculpture (McMichael 1957). There appears to be no correlation between sculpture development and habitat.

(6) *Other features.*—Colour, thickness, and texture of the periostracum, colour of the nacreous layer, thickness of the shell substance as a whole, and growth line prominence are features occasionally of use in classification, but are subject to far more variation than the features discussed above.

(ii) *Anatomy.*—Anatomical features, both macroscopic and microscopic, have been used to varying degrees in systems of classification of freshwater mussels. In particular, Simpson (1896), Ortmann (1909, 1910, 1911*a*, 1911*b*, 1911*c*), and

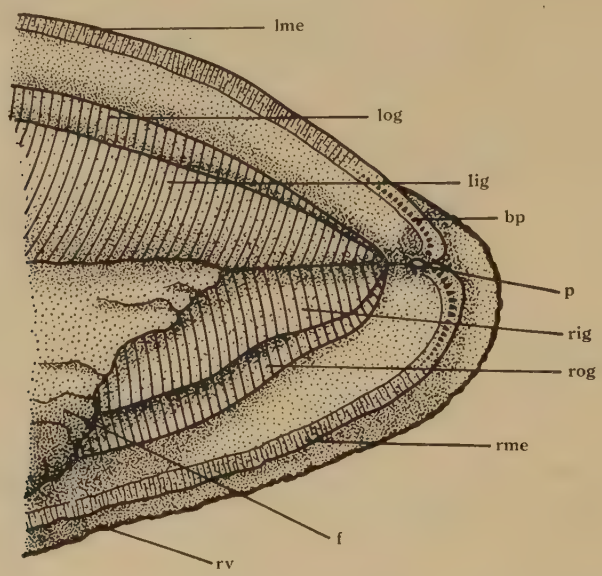

Fig. 5.—Dissection, from the left side, of the posterior end of *Alathyria pertexta pertexta* Iredale, to show the gill diaphragm and its perforation. The left gills and mantle are folded back. *bp*, branchial papillae; *f*, foot; *lig*, left inner gill; *lme*, left mantle edge; *log*, left outer gill; *rv*, right valve or shell; *p*, perforation; *rig*, right inner gill; *rme*, right mantle edge; *rog*, right outer gill.

Modell (1949) have drawn upon anatomical data. At best, anatomical features can be used to separate families and subfamilies clearly, and genera to a lesser extent, but even micro-anatomical details are of limited value at specific and subspecific level. The features of key importance are: presence or absence of a supra-anal opening, development of mantle bridges in the siphonal region, development of siphons, relative degrees of attachment of the inner and outer gills to the foot and the mantle respectively, development of a gill diaphragm, relative size and disposition of labial palps and gills, and the location of a marsupium in the gills of females and the extent of its development. Microscopic details of the gills, particularly in marsupial regions, have proved useful, but only at a level of generic separation.

Very few studies have been made previously on the anatomy of Australian mussels. Gould (1856) figured the animal of a paratype of *Unio lutulentus* (this paratype = *Hyridella aucklandica* (Gray)); Hutton (1882*a*) described *Unio menziesii*

Gray (= *Hyridella menziesi*) from New Zealand; Ortmann (1912, 1920*a*) commented on "*Hyridella australis* (L.)" (= *Velesunio ambiguus* (Philippi)); and Haas (1924) discussed *Virgus* (*Leiovirgus*) *lorentzi* Schepman (= *Hyridella misoolensis*), *Hyridella sentaniensis* Haas (= *Velesunio sentaniensis*), and (1930) *Virgus* (*Leiovirgus*) *guppyi* (Smith) (= *Hyridella guppyi*). Ortmann's were the most significant findings; he noted ten features of resemblance between *V. ambiguus* and a number of South

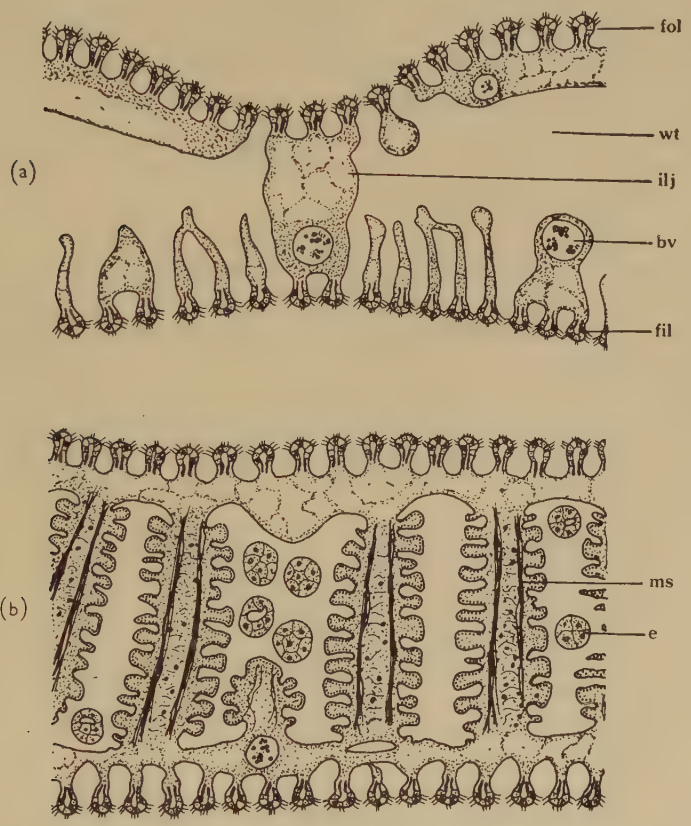

Fig. 6.—Longitudinal sections through the gills of *Velesunio ambiguus* (Philippi). (*a*) outer gill at an interlamellar junction; (*b*) inner gill in marsupial region. *bv*, blood vessel; *e*, embryo; *fil*, filament of inner lamella; *fol*, filament of outer lamella; *ilj*, interlamellar junction; *ms*, muscle strand; *wt*, water tube.

American genera, but also found two important features which allowed its separation from them. These were the development of a broad membrane around the anal opening and a small perforation in the diaphragm, a communication between the mantle and suprabranchial cavities. Such a perforation is common to practically all of the species dissected in the present work and its occurrence lends support to the notion of the indivisibility of the fauna of the Australian Region. Figure 5 illustrates the perforation in *Alathyria pertexta pertexta* Iredale.

Only Ortmann (1912) and Haas (1924) have commented upon detailed gill anatomy; Suter (1891) had commented on embryos in the inner gills of a New Zealand mussel. In the present work, microscopic details of gill anatomy, particularly of the marsupium, have been used in subfamily and generic discrimination. The features most useful in this regard are shown in Figure 6.

Modell (personal communication) has suggested that marsupial restriction to the inner gills or parts thereof may be "only a sign of swamp conditions" to allow greater oxygen uptake. The constancy of detail in the structure of the marsupium in a single species over its entire distributional range does not support this suggestion.

Of anatomical features generally, it can be said that of the characters of use taxonomically they show the least variation. Unfortunately, anatomical differences between species and genera are generally so slight that their use in the taxonomy of mussels in this region is limited.

(iii) *Larval Stages.*—Most freshwater mussel species are dioecious and reproduce seasonally, the zygote developing usually to a glochidium larva which parasitizes a fish temporarily prior to development as a free-living organism. In some South American mussels, the larva is a lasidium, originally described by Ihering (1891*a*). It is morphologically quite distinct from a glochidium, consisting of three segments of which only the middle one is covered by a shell. This larval type was believed originally to be characteristic of the family Mutelidae, but later research showed that most members of this family produced typical glochidia. Bonetto (1951) has reported the rediscovery of a lasidium; it is confined, apparently, to a few genera only of South American mussels and represents an extreme specialization. A very full summary of types of glochidia has been given by Lefevre and Curtis (1910, 1912).

Only three accounts of larval stages of Australasian mussels are known to the present authors. Suter (1891) reported finding embryos lying in the middle third of the inner gills of some specimens of *Unio* from Albury Creek and Ashburton River, New Zealand. The locality would suggest that the specimens were the "*zelebori*" form of *Hyridella menziesi*. Suter commented on the structure of the embryos, noting that they possessed "neither the sharp and angulated rudimentary shell, nor a byssus to fix themselves on the skin of fishes". He compared his observations with those of Ihering (1891*b*) on South American mussels and took them as "evidently conclusive proof of a land communication between New Zealand and South America". He also predicted that ". . . the Najadae of Australia and Tasmania will show no difference in the mode of hatching the embryos and the structure of the latter". It is evident that Suter examined either hookless glochidia or, more likely, aborted embryos at a preglochidial stage. The phenomenon of abortion on transfer of mussels to laboratory conditions is well known (Latter 1891, Hiscock 1951).

Percival (1931) gave a careful account of the glochidium of a mussel he called *Diplodon lutulentus* Gould, and noted two of its host fishes. The adult mussel shells were not figured but Professor Percival has since kindly provided us with more of the same material which proves to be *Hyridella menziesi* (Gray). The glochidia were subtriangular and hooked, 360μ long and 280μ deep, and were found on the fins, upper lip, roof of mouth, and snout of juveniles of two local species of fish, *Galaxias*

brevipennis Günth. and *Gobiomorphus gobioides* C. & V. The glochidia were found to be "ripe" during December and January.

The only record of larval stages of an Australian mainland mussel was made by Hiscock (1951). The mussel studied was *Velesunio ambiguus* (Phil.), and the callop or golden perch (*Plectroplites ambiguus* (Richardson)), a native fish, was suggested as the principal natural host fish. No evidence of seasonality in breeding was found.

In the present work, despite fairly intensive collecting, gravid females of a few species only were found. The difficulty lies in obtaining glochidia; and their close similarity, reported below, suggests that in this region larval stages are of very limited value taxonomically.

(iv) *Chromosome Studies.*—To our knowledge, no study has ever been made on chromosome characteristics of freshwater mussels, except that of Lillie (1901), who recorded a haploid number of 16 chromosomes in *Unio*. Considering the potential value of such a study in taxonomy, a number of tissues from a number of species was examined by squash technique, using a method based on that of Slizynski (1952) and staining with a synthetic orcein stain. The only nuclei that provided visible and countable chromosomes were in early to late gastrulae dissected from the marsupium of female mussels. Even then, the percentage of specimens in which the embryo cell nuclei were undergoing active mitosis was low. Consequently chromosome numbers of only three species were obtained, viz. *Velesunio ambiguus*, $2n = 34$; *V. legrandi*, $2n = 34$; and *Alathyria pertexta*, $2n = 34$. Dr. W. B. Mather, who kindly prepared the squashes of *V. ambiguus*, has classified its chromosomes as seven pairs of V's and ten pairs of J's, but reports that the centromere is difficult to locate.

This information indicates that chromosome studies within the group are possible but that they may be of limited use for taxonomy. The three species for whom the chromosome number is known are closely related. It may well be that 34 is the diploid number for all the species in the Australian region.

In general it may be stated that freshwater mussels are provided with a series of taxonomically useful characters. Since most of these characters are definable in qualitative terms only, the group as a whole is difficult to deal with systematically. Meristic characters are almost totally lacking and no other character can be used as an infallible guide to species discrimination. The whole group is remarkably plastic in response to environmental factors and the distinction between ecophenotypic differences and genetic or species differences is difficult.

(*b*) *The Species Concept in Freshwater Mussels*

(i) *The Environment and Variation.*—The number of species of freshwater mussels in the Australian Region is relatively small. In the present revision, only 29 species and four subspecies are admitted, though the number of names proposed is about three times as great. This contrasts greatly with other parts of the world, especially North America, where over 300 species are admitted from the United States alone, the area of which is a little smaller than that of the region considered here. This difference probably stems from the long isolation of the Australasian

region, the arid climate of Australia, and from the lack of knowledge of the New Guinea fauna. In compensation for the numerical paucity of species, some forms are extremely abundant and widespread. The tremendous number of populations and individuals of several species is evidence that it is not merely the lack of suitable environmental conditions which limits the number of species.

In Australia, the majority of the species are found in the relatively well-watered eastern half of the continent; the others occur mainly in the coastal streams of the south-western and north-western regions. Only one species, *Velesunio wilsonii* (Lea), occurs in the arid centre of Australia and it is apparently well adapted to withstand prolonged drought.

Whole populations are frequently affected by the peculiarities of their environment. The resulting changes are imposed directly on the phenotype and morphologically different populations of this type can be referred to as ecophenotypes. Ecophenotypical effects, as well as changes with growth, have been studied by many authors, including Ortmann (1920*b*), Ball (1922), Baker (1926, 1928), Grier and Mueller (1926), and Boycott (1936). Their results have been summarized by Eagar (1948). In general it may be stated that lake and pond populations are usually more swollen, with the shell outline more rounded and relatively higher or with the posterior end expanded and with lighter shells than their river-dwelling counterparts. Populations in fast-flowing rivers usually show more elongate shells with straight or sinuate ventral margins, less swelling and heavier teeth. The type of bottom material of the environment may also affect the form of the shell. Loose mud appears to be correlated with lightness of shells and posterior elongation, whereas coarse gravel is associated with heavier shells shortened posteriorly. Agrell (1949) regards the trophic degree of the environment as a factor of greater importance than motion of water or nature of bottom in influencing phenotype. He found that with increasing eutrophy relative weight, height, thickness, and height above midline tended to increase and the relative length of the posterior part of the shell and the ridge distance tended to decrease.

The action of environmental factors of this type can result, in time, in the evolution of a particular shell shape most suitable in a certain environment. Similar environments will produce, or tend to produce, similarly adapted populations exhibiting morphological similarities. Such ecologically adapted populations (ecotypes) are common in freshwater mussels, and such ecological adaptations may eventually become incorporated into the genotype of the species. Among the Australian freshwater mussels may be found several examples of such convergence.

The general form of appearance of a species is referred to as its facies. Modell (1949) has described three "ideal" or general types of facies which he has named anodontine, unionine, and quadruline, adapting the terms from characteristic genera. Many intermediates can be recognized, but the terms are useful nevertheless and are here defined.

Anodontine facies is characterized by light, thin shells, often swollen and with a tendency towards a spherical form. Such shells are typical of still-water environments.

Unionine facies is characterized by more elongate, heavier, and often corrugated and sculptured shells, typical of running water.

Quadruline facies is characterized by short, thick shells with extremely strong hinge structure, typical where wave action and strong currents occur.

A fourth facies type has been called *mycetopodine* and exhibits an elongate, slender shell with reduced hinge and is characteristic of burrowing species.

Most Australian species are fairly restricted in the range of shell form which their constituent populations can develop, but a few species are widespread and highly adaptive and can exhibit a wide range of facies. In Australia, *Velesunio ambiguus* and in New Zealand, *Hyridella menziesi* can be cited as examples.

(ii) *Speciation in Freshwater Mussels.*—The concept of polytypic species composed of geographically representative races, which has developed primarily from the study of terrestrial vertebrates, cannot be transferred *in toto* to every other animal group. Within the terrestrial environment, there is more or less widespread continuity of the environment which allows gene flow to proceed between adjacent populations at a reasonable rate. If the gene flow is interrupted by definite geographic barriers to a stage where some form of reproductive isolation is established, speciation can occur. Furthermore, the principal factors responsible for selection and genetic differentiation of populations are climate, vegetation, etc., factors which tend to be fairly uniform over large geographic areas. As a result, populations tend to become genetically divergent in a similar way over large areas and geographic races develop which are easily recognizable.

In the freshwater environment, only large river systems provide a continuous medium for long distances where gene flow can proceed between populations at a reasonable rate. A considerable number of freshwater environments, however, including many of the smaller ponds and all of the coastal rivers and streams, are isolated from each other by land masses or sea. Although transfer of mussels by birds between adjacent populations probably results in sufficient gene exchange to prevent speciation, the exchange seems to be sufficiently limited to restrict rapid spread of genes and does not necessarily maintain genetic uniformity between populations.

The principal selective factors in the freshwater environment are not uniform over wide areas, but differ from stream to stream. Each stream, and parts of each stream, differ in calcium content, speed of flow, nature of bottom materials, turbidity of water, water temperature, and trophic degree. Thus the population of each river, as well as exhibiting ecophenotypic variation and adaptation, tends to become genetically adapted to its particular environment and the limited gene flow between neighbouring populations prevents any marked degree of fusion of these differences over a broad geographic area.

Thus it is not easy to define geographic races in freshwater mussels unless the population of each isolated river and pond which happens to be recognizably different from its neighbours is given a separate subspecific name. On the other hand, it cannot be assumed that speciation occurs by any process other than the normal process of geographic isolation and selection in this group. It is necessary to consider briefly the criteria which must be used in recognition of species and subspecies.

(iii) *The Species Concept.*—It is frequently difficult to distinguish between ecophenotypic variants, genetically adapted ecotypes, and species. Ecophenotypes

have often been recognized as separate species. A classic case of such taxonomic "splitting" among the freshwater mussels of France was discussed by Schnitter (1922). From among the two or three valid species which occur there, 208 species of *Unio* and 250 species of *Anodonta* were recognized. If genetically divergent forms are recognizable—and this can result only from large-scale population studies—the problem arises what taxonomic recognition they should receive. The ecotype inhabiting an isolated river system, such as a coastal stream, is the biological equivalent of the terrestrial subspecies. However, similar ecotypes are likely to occur wherever stream conditions are similar. To recognize each genetically adapted variant would result in the naming of a number of polytopic subspecies. We feel that the naming or recognition of such polytopic races is of little value taxonomically and does nothing to indicate the types of genetic processes occurring within the species structure. We have, therefore, avoided the general use of a trinomial system, though we have referred to such forms under the latinized names which have already been given them. For example in *Velesunio ambiguus*, we use the term "*evansi* form" for the particular ecotype to which the specific name *evansi* was originally applied. We do not record such forms as valid subspecies, though the application of the principles for polytopic subspecies, laid down by Mayr, Linsley, and Usinger (1953, p. 32), would probably result in their being recognized as such.

In the present work subspecific recognition is given only in those cases where geographically distinct groups of populations show morphological differences from other populations of the species and the differences are genetically determined, as far as we can tell. These are few and far between in freshwater mussels in this region. The problem of whether to recognize such groups as full species or subspecies is difficult to solve without experimental evidence on the degree of reproductive isolation of the groups in question. In none of the cases of possible subspecies admitted here as full species is there intergradation of form or complete continuity of range, as far as available material has shown.

The species concept adopted here is one of widespread, variable species, with some genetically divergent populations; these, however, are not recognized nomenclaturally unless they occur over a considerable geographic area and occupy a range more or less distinct from that of the parent population.

III. Taxonomy of Recent Species

(*a*) *Remarks*

In the following account, a uniform procedure has been adopted, as far as possible, in the description of each taxon. The groups are arranged in part according to possible evolutionary relationships, in part for convenience. The higher classification of the group will be discussed later when possible relationships and phylogeny of the Australasian groups are dealt with.

Synonymies are for the most part restricted, references being included only when the specimens referred to could be determined with accuracy by us, either from figures or the original material. For each synonym the type locality given by the original author is given and where necessary has been restricted or adjusted.

In the tables of dimensions, measurements given were made from actual specimens wherever possible. In some cases dimensions (where indicated) are from the original description, figures, or photographs which, unless otherwise indicated, were taken to be of natural size.

Under the heading "*Material Examined*", the localities of all the series examined personally by one or both of the authors are given. For brevity's sake, data on collector, date, and institution in which the shells are housed are omitted. Nearly all the series examined in the present work bear labels with our identification. For type material, the parent institution, registered number, and type locality are given. The names of the several institutions are abbreviated thus:

AM	Australian Museum, Sydney;
AMNH	American Museum of Natural History, New York;
ANSP	Academy of Natural Sciences, Philadelphia;
BM	British Museum (Natural History), London;
CMP	Carnegie Museum, Pittsburgh;
CNHM	Chicago Natural History Museum, Chicago;
DMW	Dominion Museum, Wellington;
MCZ	Museum of Comparative Zoology, Cambridge, Mass.;
MNHN	Muséum National d'Histoire Naturelle, Paris;
MZUM	Museum of Zoology, University of Michigan;
NMV	National Museum of Victoria, Melbourne;
QM	Queensland Museum, Brisbane;
QVML	Queen Victoria Museum, Launceston;
SAM	South Australian Museum, Adelaide;
USNM	United States National Museum, Washington;
ZDQ	Zoology Department, University of Queensland, Brisbane.

Each taxon has been redescribed according to a formula designed to bring uniformity. In some cases, original descriptions were full and adequate, but frequently, redescription has been necessary to meet the demands of the formula. Photographic illustrations of the types of most species and synonyms have been given; many have not been illustrated thus previously.

No key to the species is included. The reasons for this omission are several. The primary taxonomic character, the beak sculpture or its absence, can rarely be determined without a large series of shells because the beaks are nearly always corroded and inclusion of this character in a key would render it unworkable for small samples. The second most important character, shell form, is highly variable in practically every species, and again its use in a key would demand large samples. The species lack meristic characters and can seldom be discriminated by a single criterion. Anatomical features, though they have proved of use in the present work in diagnosis of the higher taxa, are never significant at the specific level, and the larval stages are, as yet, inadequately known. We do, however, believe that the species here recognized, based as they are in most cases on the study of very large series, are discrete taxonomic units, and can be recognized easily by the student familiar with the group. As an aid, a differential diagnosis of species is given for each genus.

(*b*) *Taxonomy*

Family **MUTELIDAE** Gray 1847

Freshwater mussels of variable facies, primitively without beak or shell sculpture, but some groups developing both; hinge primitively lamellar, sometimes developed to complex unionid, sometimes reduced; siphons generally well developed, supra-anal and anal fused, mantle bridge between anal and branchial well developed, branchial rarely closed below; marsupium in inner gills, variously developed; larva a glochidium or lasidium.

Distribution

South Africa, South America, New Zealand, New Guinea, Australia, Solomon Islands.

Subfamily **VELESUNIONINAE** Iredale

Subfamily Velesunionae (*sic*) = Velesunioninae Iredale, 1934, p. 58.

Remarks

Iredale established the subfamily to include all the Australian mussels with unsculptured beaks, with the exception of *Lortiella* Iredale, an aberrant genus from north-western Australia. He correctly recognized the absence of beak sculpture as an important taxonomic character. The original diagnosis read simply "beaks smooth", while the subfamily Lortiellinae was diagnosed as "beaks ridged". Since the beaks of the latter group are apparently smooth, the subfamilies must be defined more precisely if they are to stand.

As originally proposed, the subfamily Velesunioninae included five genera, viz. *Velesunio* Iredale, *Alathyria* Iredale, *Westralunio* Iredale, *Centralhyria* Iredale, and *Hyridunio* Iredale. Iredale (1943*b*) noted that juvenile *Hyridunio* possessed sculptured beaks and transferred the genus to the subfamily Propehyridellinae Iredale. He also (1943*a*) raised *Aparcthyria*, a subgenus of *Centralhyria*, to generic rank and named an additional genus *Quaesithyria*.

In the present work, only three of these genera are admitted: *Velesunio* with *Centralhyria* and *Aparcthyria* as synonyms, *Alathyria* with *Quaesithyria* as a synonym, and *Westralunio*; and the New Guinea genus *Microdontia* Tapparone Canefri is added to the group.

Diagnosis

Freshwater mussels of the family Mutelidae of variable facies, with unsculptured beaks and relatively simple outline. Hinge primitively lamellar but developing to a unionid type in some species. Anterior retractor and adductor muscle scars fused. Supra-anal opening absent, siphons not prominent or protruding, gill diaphragm perforate. Marsupium always present in inner gills of females and occupying at least two-thirds of the gill. Interlamellar junctions of marsupium often reduced to discontinuous septa, characteristically closely packed, with dense connective tissue, folded epithelium and well-developed muscle strands. Glochidium subtriangular, hooked; host-fishes mostly unknown.

Present Distribution

Australia (including Tasmania) and New Guinea.

Fossil Record

Apparently represented in New Zealand in the Tertiary and in Australia since the Triassic (McMichael 1957).

Genus VELESUNIO Iredale

Velesunio Iredale, 1934, p. 59. Type species by original designation: *Unio balonnensis* Conrad 1850 (= *Unio ambiguus* Philippi, 1847).

Centralhyria Iredale, 1934, p. 65. Type species by original designation: *Unio stuarti* Adams & Angas 1864 (= *Unio wilsonii* Lea, 1859).

Aparcthyria Iredale, 1934, p. 67. Type species by original designation: *Unio angasi* Sowerby, 1867.

Remarks

This genus, the most widespread and abundant of Australian freshwater mussels, occurs also in New Guinea, but not, curiously, in New Zealand. Iredale (1934, 1943*a*, 1943*b*) admitted 14 species under the three generic names above. In the present work, five species are recognized, four as of Iredale (loc. cit.) and one from New Guinea, not previously located here. If all three genera above were allowed to stand, the five species would be located as follows: two in *Velesunio*, one in *Centralhyria*, and two in *Aparcthyria*. Examination of large series of mussels of these groups has revealed a close conchological and anatomical similarity between them and no grounds, other than geography, on which continued generic segregation would be justified. The genus includes all the velesunionine mussels which are relatively small, with simple lamellar hinges, typically thin shells and weakly impressed muscle scars. The other genera in this subfamily are fairly strongly contrasted to *Velesunio*. Admittedly, old shells of *V. legrandi* approach *Alathyria* in character and *A. profuga* approaches *Velesunio*, but the young shells are easily diagnosed.

The genus *Velesunio* is the group erroneously considered by most authors as *Hyridella* Swainson, s.s. The nomenclatural complications of this error have been discussed by McMichael (1955) and are discussed further below.

Diagnosis

Shell Characters.—Freshwater mussels of the subfamily Velesunioninae of small to large size. Shells generally rounded, sometimes slightly winged posteriorly, BHI never less than 80 per cent., maximum length not greater than twice maximum height. Hinge straight or gently curved, weak to strong lamellar; teeth usually simple, thin and smooth, sometimes serrated, occasionally reduced. Beaks always smooth, shell substance typically thin, thick and heavy in some old shells. Shells usually of medium width, sometimes greatly swollen, but not exhibiting sexual dimorphism in this regard. Muscle scars usually lightly impressed, rarely strongly so, anterior adductor and retractor fused; pallial line always prominent.

Anatomy.—Supra-anal opening absent; siphons of moderate size but not prominent; anal smooth, branchial papillate with up to 5 rows of medium-sized papillae; branchial opening about $1\frac{1}{4}$ times size anal and open below; siphons separated by prominent mantle bridge, the whole area usually pigmented. Labial palps of medium size, triangular or subtriangular, and free except on dorsal border. Outer lamellae of outer gills completely fused to mantle; inner lamellae of inner

gills fused to visceral mass, and united, posterior to visceral mass, connecting to mantle bridge to form a diaphragm which is always perforate; diaphragm relatively short. Outer gills subtriangular and free at edges except on dorsal border, internally undifferentiated with weakly developed interlamellar junctions. Inner gills fused dorsally and anteriorly to visceral mass but not to labial palpi; internally undifferentiated in male, but always exhibiting marsupial development in the middle two-thirds in females; interlamellar junctions in marsupium close together, and showing moderate muscular development (Plate 17, Figs. 2 and 3).

Glochidium.—Subtriangular and hooked when fully developed. No evidence of seasonality in breeding.

Distribution

Throughout south-eastern, eastern, and northern Australia (except for some coastal rivers of New South Wales), the Tamar River system in northern Tasmania, and north-eastern New Guinea.

Differential Diagnosis of Species

The New Guinea species, *V. sentaniensis*, is a small, thin mussel, elongate-elliptical and deflected ventrally at the posterior end and with a BLI of 25 per cent. The four mainland species are distinguished thus: *V. wilsonii* is long with almost parallel dorsal and ventral margins, MHI of 50 per cent., and an acuminate posterior end; *V. angasi* is a higher shell with a fairly pronounced wing, BHI of *c.* 80 per cent., and a prominent posterior ridge; *V. ambiguus* resembles *V. angasi* but lacks any marked winging, its BHI is not less than 90 per cent. *V. legrandi* is large, expanded posteriorly, somewhat winged, BHI of *c.* 80 per cent., possesses a strong hinge and heavy cardinal teeth, deeply impressed muscle scars and is confined to Tasmania.

Relationships

Velesunio is closely related to *Alathyria* and *Westralunio*. *Alathyria* differs in being heavier and possessing a strong unionid hinge whilst *Westralunio* is small but has very strong grooved cardinal teeth.

Velesunio ambiguus (Philippi)

Plate 1, Figs. 1–14; Plate 2, Figs. 1–5; Plate 17, Figs. 2 and 3

Unio ambiguus Philippi, 1847, p. 7(47), pl. 3, fig. 2. Sowerby, 1867*a*, pl. 69, sp. and fig. 355. Smith, 1881, p. 309.

Unio balonnensis Conrad, 1850, p. 10; 1854, p. 295, pl. xxvi, fig. 5.

Unio vittatus Lea, 1859, p. 153; 1860, p. 249, pl. 38, fig. 128. Reeve, 1864, pl. xviii, sp. and fig. 83. Tate, 1887, p. 101.

Unio philippianus Kuster, 1861, p. 235, pl. 79, fig. 2. (New name for *U. ambiguus* Philippi.)

Unio (*Alasmodon*) *evansi* A. Adams & Angas, 1864, p. 39.

Unio evansi A. Adams & Angas, Sowerby, 1867*a*, pl. lvi, sp. and fig. 285. Smith, 1881, p. 312. Tate, 1887, p. 101.

Unio jeffreysianus Lea, 1871, p. 188; 1874, p. 23, pl. vii, fig. 20. Smith, 1881, p. 311.

Unio danellii Villa, 1871, p. 328. Smith, 1881, p. 311. Fischer-Piette, 1950, p. 77, pl. 4, fig. 72, pl. 5, figs. 73 and 74.

Unio australis Lam., Smith, 1881, p. 309. (Non *U. australis* Lamarck 1819.)

Hyridella australis (Lam.), Ortmann, 1912, p. 100. Cotton and Gabriel, 1932, p. 155, pl. xvi, fig. 1. Cotton, 1934, p. 113, pl. 2. Cotton and Godfrey, 1938, p. 88. fig. 74. Gabriel, 1939, p. 129, pl. iv, fig. 38. Hiscock, 1951, pp. 146–8. (All non *U. australis* Lamarck.)

Diplodon (*Hyridella*) *vittatus* (Lea) Simpson, 1914, p. 1296.
Diplodon (*Hyridella*) *evansi* (A. Adams & Angas) Simpson, 1914, p. 1303.
Diplodon (*Hyridella*) *australis* (Lam.) Simpson, 1914, pp. 1297–8. (Non *U. australis* Lamarck.)
Diplodon (*Hyridella*) *jeffreysianus* (Lea) Simpson, 1914, p. 1299.
Hyridella ambigua (Phil.) Ortmann, 1920*a*, pp. 119–21. Cotton and Gabriel, 1932, pp. 156–7, pl. xvi, fig. 2. Cotton and Godfrey, 1938, pp. 88–9, fig. 75.
Unio protovittatus Hale & Tindale, 1930, p. 154, fig. 9. (Subfossil).
Velesunio balonnensis (Conrad) Iredale, 1934, pp. 59–60, pl. iii, fig. 1. pl. iv, fig. 1. McMichael, 1952, p. 350.
Velesunio balonnensis intricatus Iredale, 1934, p. 60, pl. iii, fig. 2, pl. iv, fig. 2.
Velesunio balonnensis adjunctus Iredale, 1934, p. 59, pl. iii, fig. 3, pl. iv, fig. 3.
Velesunio evansi (A. Adams & Angas) Iredale, 1934, p. 62, pl. iii, figs. 6 and 7, pl. iv, figs. 6 and 7. McMichael, 1952, p. 398.
Velesunio danellii (Villa) Iredale, 1934, p. 60, pl. iii, fig. 4, pl. iv, fig. 4. McMichael, 1952, p. 398. Kershaw, 1956, p. 52.
Velesunio adjunctus Iredale, 1943*b*, p. 88.
Velesunio mckeowni Iredale, 1943*b*, p. 88, fig. 1.
Velesunio testatus Iredale, 1943*b*, pp. 88–9. Kershaw, 1956, pp. 52–3.
Velesunio transitus Iredale, 1943*b*, p. 89.

Remarks

The large number of synonyms indicates the variability of this abundant and widely distributed species. Since many of the named forms regarded here as synonyms have been considered as separate species by recent authors, discussion of specific synonyms seems warranted.

U. ambiguus Philippi: Has been used for several species. Smith (1881) correctly applied the name to the common *Velesunio* of the inland rivers of New South Wales and from the Onkaparinga River at Noarlunga, South Australia. He correctly synonymized *Unio balonnensis* Conrad, *U. philippianus* Kuster, and *U. vittatus* Lea and noted that Philippi's figure was not of an adult specimen. Simpson (1914) regarded the earlier name *U. australis* Lam. as applying to this form and placed *U. ambiguus* as a synonym. Cotton and Gabriel (1932) and Cotton and Godfrey (1938) followed Simpson in the application of *U. australis* Lam. for the common *Velesunio*, but regarded lagoon forms from the Murray River as distinct. Adams and Angas (1864) had named these forms *U. evansi*, but Cotton and Gabriel considered that *U. ambiguus* applied to them, and used "*ambiguus*" in that sense. Iredale (1934) applied "*ambiguus*" to a Western Australian species, erected a new genus, *Westralunio*, to accommodate it, and selected King George's Sound as restricted type locality. At the same time he described a subspecies, *W. ambiguus carteri*. The name *ambiguus* cannot apply to the Western Australian forms which are characterized by heavy, grooved cardinal teeth, whereas the holotype possesses simple lamellar cardinals. As discussed below, the subspecific name *carteri* must be elevated to specific rank for the Western Australian species.

A photograph of the holotype of *U. ambiguus* from the British Museum has clarified details of internal shell structure, not clear in Philippi's figure, and leaves no doubt that the name is correctly applied here.

U. balonnensis Conrad: This name has always been correctly applied to the common *Velesunio* of inland New South Wales, Conrad's description and figure and

precise type locality leaving no doubt as to its identity. Iredale (1934) used this name as the valid name for *U. ambiguus*, placing the latter elsewhere. Most other authors have synonymized *U. balonnensis* under "*australis*" or "*ambiguus*". It is definitely the same as *V. ambiguus*.

V. balonnensis intricatus Iredale: This name was provided for a series of thin-shelled, swollen, lagoon-dwelling shells from the central coast of Queensland. Iredale admitted their similarity to typical *balonnensis* and examination of a large series of shells from Rockhampton reveals that there are no features of systematic worth to separate this form.

V. balonnensis adjunctus Iredale: Shells from the Richmond River, New South Wales, were separated subspecifically on the basis of acute angulation anteriorly and sharp, oblique truncation of the posterior margin. Typical *V. ambiguus* is found in the same region, as well as many intermediate forms. Though *adjunctus* may represent a somewhat genetically distinct group of mussels, it cannot have reached any degree of reproductive isolation nor can it be regarded as a geographic subspecies.

U. vittatus Lea: This name was based on two specimens, the holotype, the larger, in the Cuming collection, which was figured by Lea (1860) and subsequently by Reeve (1864), and a smaller paratype retained by Lea. Specimens from Lake Alexandrina, lower Murray River, match the figured specimen in every respect and leave no doubt that the specimens described by Lea came from this area. The Lake Alexandrina specimens are intermediate between typical *V. ambiguus* and "*evansi*" forms. The paratype differs considerably from the holotype; it resembles closely shells found further inland. Most authors have regarded *U. vittatus* as a synonym of *ambiguus*. Iredale, however, noted a superficial resemblance between *vittatus* and *U. shuttleworthi* Kuster and regarded *vittatus* as Tasmanian. No Tasmanian shells possess a yellowish olive periostracum, typical of *vittatus*, so that Lea must have named mainland shells.

U. philippianus Kuster: Proposed as a substitute name for *U. ambiguus* Phil. Kuster included *Castalia ambiguus* Lam. in the genus *Unio*, making *ambiguus* Phil. preoccupied. Kuster apparently figured Philippi's type when renaming the species.

Unio (*Alasmodon*) *evansi* Adams & Angas: The name was given to a thin shell, winged dorsally at the posterior end, from a lagoon of the lower Murray River. It differs in appearance from typical *V. ambiguus* and has been regarded by many authors as distinct (Smith 1881; Simpson 1914; Cotton and Gabriel 1932; Iredale 1934; Cotton and Godfrey 1938). There is no doubt that the lagoon-dwelling forms especially of the lower Murray River tend towards an "*evansi*" form, and Cotton and Gabriel (1932) and Cotton and Godfrey (1938) attempted to differentiate between it (calling it *Hyridella ambigua*) and the typical form (calling it *H. australis*) on the basis of different distribution and different relative width (or section) of the shells. Those shells with a length about $2\frac{1}{4}$ times the width were called *australis*; with a length about 3 times the width were called *ambigua*. Examination of large series of shells from all parts of the Murray River has revealed intergrades between the two forms (see Fig. 7). *U. evansi* is regarded here as an ecophenotypical variant. The type series consists only of holotype and one paratype. As stressed below, the extreme variability

of *V. ambiguus* demands consideration of large series of shells and not individual variants.

U. jeffreysianus Lea: Based on a shell from Australia which possessed a single lateral tooth in each valve. From the measurements and description, Iredale (1934) assumed, probably correctly, that it was the same as *U. danellii* Villa.

U. danellii Villa: Name given to a shell from "Australia meridionale, in rivulo prope Brunswick" i.e. Yarra River, Victoria, at Brunswick. *U. jeffreysianus* is almost certainly the same. Iredale used the name *danellii** for the velesunios from

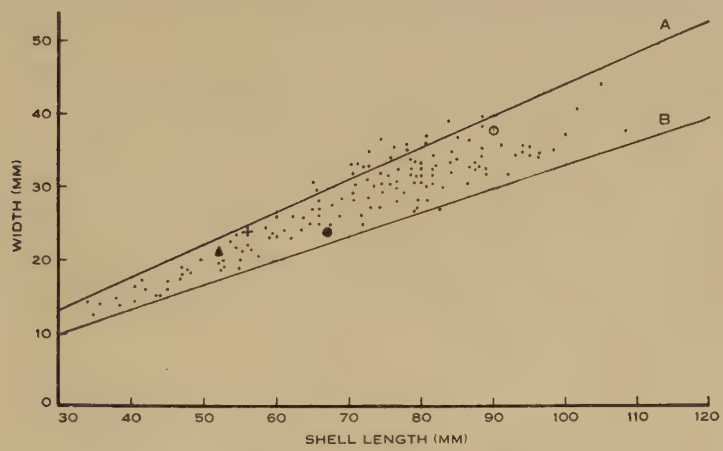

Fig. 7.—Scatter diagram showing the relation of shell length to width in a population of *Velesunio ambiguus* (Philippi) from the lower reaches of the Murray River. Line *A* represents a length–width ratio of 2¼, line *B* a ratio of 3. The symbols represent several forms thus: ▲, *V. ambiguus*, holotype; +, *U. evansi*, typical form; ●, V. *testatus*, holotype; and ○, *V. mckeowni*, holotype.

Victorian coastal streams. However, we have examined large series of shells in the National Museum, Melbourne, which reveal that the majority of Victorian populations are typical *V. ambiguus*, the Yarra River form being an ecophenotype only. Fischer-Piette (1950) has recently figured the holotype of *U. danellii*.

U. (*Hyridella*) *protovittatus* Hale & Tindale: Name applied to subfossil shells from Tartangan Beds, lower Murray River, separated specifically from present-day forms by their thicker marginal shell substance. This material represents an old lagoon-dwelling population of shells of the "*evansi*"–"*vittatus*" form discussed above. The thickness of the shells is not of taxonomic importance in this species; in any case, aging of the shells causes swelling of the shell substance, particularly the nacreous layer.

V. mckeowni Iredale: Name given to a population of large shells, from the Murrumbidgee River, with a slight angulation posteriorly. Shells from several

*Iredale's use of *danellii* as the prior name was incorrect. Lea's description of *U. jeffreysianus* was published on October 24, 1871, while Villa's description appeared on December 6, 1871, as revealed by the corrected dates of publication recently issued by the Journal de Conchyliologie.

populations in the Murrumbidgee River show complete intergrading from typical *ambiguus* to this form which cannot be considered as distinct.

V. testatus Iredale: Iredale (1934) identified all the thin-shelled mussels from the lower Murray River as *V. evansi*. In a later paper (1943*b*) he restricted *evansi* to the rounded forms and erected *testatus* for the remainder of the thin-shelled forms. The type series of *V. testatus* differ from typical *ambiguus* only in being thin-shelled and slightly more elongate and cannot be separated taxonomically.

V. transitus Iredale: Name applied by Iredale (1943*b*) to a series of populations of *Velesunio* from coastal streams around Sydney, in the belief that the same species could not be found in different river systems. The shells are in no way distinguishable from typical *V. ambiguus*.

U. australis Lam.: Philippi (1847) redescribed and figured a shell as *U. australis* Lam. but was obviously in error. The shell figured is a *Velesunio*, very similar to *V. legrandi* from Tasmania. Smith (1881) adopted Philippi's idea of it and several more recent authors, as listed above, have followed him. It has been shown (McMichael 1955) that this name has nothing to do with the present species, but belongs to the subfamily Hyridellinae. Ortmann (1912) used the name *Hyridella australis* (Lam.) when publishing notes on the anatomy of some mussel specimens from Gippsland, Victoria, but did not figure the shells. These are in the Carnegie Museum, Pittsburgh, and are typical *V. ambiguus* Phil.

Types

U. ambiguus Phil.: Holotype BM Reg. No. 41-4-29-103. Original type locality: Nova Hollandia. Iredale's (1934) restriction of type locality to King George's Sound, W.A., must be disregarded, for reasons outlined above. Exact type locality undetermined.

U. balonnensis Conrad: Holotype ANSP Mus. No. 189249. Type locality: Balonne R., Australia. Paratype MCZ Reg. No. 72078.

U. vittatus Lea: Holotype BM unregistered. Original type locality: Australia. Paratype USNM No. 84407. Type locality here restricted to lower Murray R., S.A.

U. evansi Adams & Angas: Holotype BM Reg. No. 1870-10-26-42. Type locality: Lagoons of lower Murray R., S.A.

U. jeffreysianus Lea: Holotype USNM No. 84849. Original type locality: Australia. Restricted by Iredale (1934) to R. Yarra, Vic.; here accepted.

U. danellii Villa: Fischer-Piette (1950) has located the holotype in the collection of the Journal de Conchyliologie. Type locality: Brunswick, R. Yarra, Vic.

U. protovittatus Hale & Tindale: Holotype SAM Reg. No. P. 178. Paratype SAM Reg. No. P. 178. Type locality: Tartangan Bed, Layer C, Murray R., S.A.

V. mckeowni Iredale: Holotype AM Reg. No. C. 61721. Paratypes C. 61721, C. 61680. Type locality: Leeton, Murrumbidgee R., N.S.W.

V. testatus Iredale: Holotype AM Reg. No. C. 61699. Paratypes C. 61723, C. 61698. Type locality: Benthagi, Murray R., N.S.W.

V. transitus Iredale: Holotype not selected. Syntypes AM. Lectotype, here selected, Reg. No. C. 61691. Type locality: Camden, Nepean R., N.S.W.

V. adjunctus Iredale: Holotype Reg. No. AM C. 12003. Paratypes C. 61708. Type locality: Richmond R., N.S.W.

V. balonnensis intricatus Iredale: Holotype AM Reg. No. C. 61725. Type locality (here restricted): Rockhampton, Qld. Paratypes from Rockhampton (C. 61889) and Port Curtis (C. 47293).

Description

No single description of this species can ever be complete and entirely satisfactory. The species can be understood adequately only on the basis of a study of a

large number of populations covering the distributional range of the species. In the past, as outlined above, single shells or small populations, considered, as it were, out of context, have been described as new. In the present study, several groups of shells, quite atypical of *V. ambiguus*, have come to hand. In each case, their restricted habitat demands their recognition as ecophenotypic variants only.

Shell Morphology.—Shells of variable size, ranging up to 105 mm long, maximum height up to 65 mm, MHI usually 58–69 per cent. Width ranging from extremely compressed and thin to globosely swollen, but exhibiting no sexual dimorphism in this respect. Typical outline elongate-oval with relatively long anterior end, BLI about 30 per cent., tending to decrease in specimens in higher latitudes. Anterior margin rounded; posterior margin variably so and slightly more pointed; dorsal margin posterior to the beaks usually a little elevated producing only slight winging, BHI typically about 90 per cent.; ventral margin slightly to noticeably rounded, rarely straight, continuing evenly with anterior and posterior margins. Beaks swollen or depressed, usually strongly eroded in large or old shells, unsculptured at any stage. Posterior ridge prominent only in swollen shells.

Periostracum varying from yellowish olive to dark brown, sometimes smooth and polished, sometimes rough, and marked by coarse growth lines. Nacre usually flat white, often marked by purple, pink, orange, or brownish spots; shell ranging from thin and fragile to thick and strong.

Hinge varies from weak to moderately strong, typically lamellar; lateral teeth long, slender, and slightly curved, double in the left valve, the upper tooth shorter, all laterals tapering fairly sharply posteriorly; cardinal teeth smooth and straight, up to 30 per cent. of length of laterals, paired in right valve, the upper tooth the weaker, often rudimentary. In very large shells the teeth are heavy, especially the cardinals, which tend to be curved and slightly grooved.

Posterior muscle scars lightly impressed, adductor and retractor fused; anterior scars weak to moderately strong, especially in large shells, partly fused but distinct. Pallial line always prominent.

Anatomy.—With the characters of the genus. Siphons not prominent, branchial about $1\frac{1}{4}$ times size anal and bearing 4–5 rows of medium-sized papillae internally, the inner row of 5–7 larger papillae. Palps of medium size, subtriangular, pointing posteriorly. Marsupium well developed, occupying middle two-thirds of inner gill in non-gravid females. In fully gravid females, all of the inner gill is occupied by glochidia. Outer gill in both sexes looped but with very few interlamellar junctions, which when present are poorly developed. Both lamellae possess long prominent interfilamentar junctions, well vascularized with large vertical vessels, and with simple smooth epithelium. The ventral margin is rounded. Inner gill of females is thicker, not looped, and with frequent interlamellar junctions. In the marsupium, these are close together and well developed, with heavily folded epithelium and prominent muscle bands crossing between the lamellae. The ventral margin is grooved. Chitinous supporting rods of the filaments long, usually incomplete, thin in section, lying at the base of the filaments (Plate 17, Figs. 2 and 3).

Glochidium.—Subtriangular, swollen, measuring approximately 250μ in the hinge plane and 220μ deep. Hooks on ventral border to one side of centre. The report of hookless glochidia for mussels from the lower Murray River (Hiscock 1951) requires modification. A re-examination of this material and of material which has come to hand since shows that the hooks develop late and glochidia within their vitelline membrane usually appear hookless. The original report refers to prematurely released larvae; fully developed, free glochidia of *V. ambiguus* are always hooked.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. ambiguus Holotype	52	17	33%	34	65%	31	91%	21
U. balonnensis Holotype ex photo.	60	20	33%	36	60%	34	94%	24
U. vittatus Holotype	64	16	25%	42	66%	39	93%	23
U. evansi Holotype	58	20	34%	40	69%	37	92%	?
U. jeffreysianus Holotype	72	24	33%	45	61%	41	91%	24
U. danellii Holotype, ex photo. Fischer-Piette	90	25	28%	53	59%	50	94%	34
V. balonnensis intricatus Holotype	75	21	28%	46	62%	41	89%	28
V. balonnensis adjunctus Holotype	73	25	34%	44	60%	42	95%	22
V. mckeowni Holotype	90	28	31%	58	65%	54	93%	38
V. testatus Holotype	67	22	33%	40	60%	36	90%	24
V. transitus Lectotype	64	20	31%	38	59%	34	90%	26
Mean 126 specimens, Condamine R., Warwick; ZDQ	76	25	32%	48	63%	42	88%	35
Mean 50 specimens Aramac; ZDQ	77	23	30%	41	53%	37	91%	25
Mean 74 specimens, Mannum, Murray R.; ZDQ	73	20	28%	46	64%	39	85%	30

Material Examined

Type material as above, and from QUEENSLAND: Burdekin R., Charters Towers; Enoggera Ck.; Waraba Ck., Caboolture; Gin Gin Ck., Gin Gin; Oxley Ck., Brisbane; Mary R., Baramba; Burnett R., Watalgan; Baffle Ck., Miriam Vale; Calliope R., Port Curtis; Fitzroy R., near Rockhampton; Murray Lagoons, near Rockhampton; Bulloo R., Thargomindah; Warrego R., Charleville, Cunnamulla; Dumaresque R., Texas; Condamine R., Dalby Ck., Springvale, Miles, Deuchar Ck., Warwick, Cecil Plains; Isis R., Childers; Albert R.; Diamentina R.; Alice R., Barcaldine; Macintyre R., Goondiwindi; Kolan R.; Gowrie Ck. (Darling Downs); King's Ck. (Darling Downs); Herbert R. Gorge; Logan R., Pimpama, Walker's Lagoon; Ross R., Townsville; Balonne R., St. George, Bindle; Blackwater Ck., Adavale; Aramac Ck., Aramac; Moonie R., Thallon; Brisbane R., Wyvenhoe; Lake Manchester; Jordan R., Jericho; Bungil Ck., Roma;

Pioneer R., Mackay. NEW SOUTH WALES: Dumaresque R., Boggabilla; Macintyre R., Inverell; Lake Narran; Moonie R., Mogil Mogil; Barwon R., Collarenebri, Walgett, Brewarrina; Darling R., Bourke, Pooncarrie; Namoi R., Narrabri; Peel R., Tamworth; Castlereagh R., Gilgandra; Macquarie R., Dubbo, Warren, Gunningbar Ck., Dundallamel, Lucknow; Bogan R., Peak Hill, Nyngan; Abercrombie R., Burraburra Ck.; Lachlan R., Hillston; Lake Talbot, Narrandera; Murrumbidgee R., Leeton, Wagga, Griffith; swamp near Yanco; Ginninderra Ck., near Canberra; Billabong Ck., Culcairn, Wanganella; Murray R., Hume Reservoir, Benthaggi; Edwards R., Deniliquin; Richmond R.,; Clarence R., Woodenbong; Bardens Ck., South Grafton; Myrtle Ck.; Eastern Ck., Quaker's Hill; South Ck., near Sydney; Rope's Ck., near Sydney; Kemp's Ck., near Liverpool; Nepean R., Camden, Picton; Georges R., Liverpool; Wollondilly R.; Umeralla R., Cooma. VICTORIA: Murray R., Wodonga, Merbein, Chalka Ck., Echuca, Mondellin; Lake Lonsdale; Goulburn R., Merrigum, Rialla; Broken Ck., Benalla; Gunbower Ck., Wee Wee Rup; Box Ck., Cohuna; Loddon R., Serpentine Ck., Avoca; Wimmera R., Horsham; Muddy Ck.; Mitchell R., Bairnsdale; Latrobe R., Sale; Moe R., Moe; Yarra R., Melbourne, Bangham Waterholes, Melbourne Falls, Watson's Ck., Diamond Ck., Merri Ck., Yallock Ck.; Gardinia Ck., Beaconsfield; Mordialloc Ck.; Frankston Ck., Frankston; Altona Bay; Moorabool R., Lal Lal Falls, Batesford, Kooleycohghurt Ck.; Barwon R., Birregurra, Winchelsea; Emu Ck., Skipton; Tyers R.; Ovens R., Wangaratta; Werribee R.; King R.; Lake Murtoa; Narcooya Ck.; Saltwater Ck., Keilor Plains; Glenelg R., Dartmoor; Lachlan R., Hillston; Yan Yean Reservoir; Lake Wendouree; Bass R.; Sealer's Ck., Wilson's Promontory. SOUTH AUSTRALIA: Onkaparinga R.; Gawler R.; North Para R.; South Para R.; Para R.; Currency Ck.; Torrens R.; Lake Euston; Lake Culluleraine; Murray R., Lake Alexandrina, Murray Bridge, Tailem Bend, Tartanga Lagoon, Barmera, Mannum, Milang, Lake Bonney, Port Sturt, Sunnyside, Swan Reach; Hope Valley Reservoir; Breamer R.; Light R.; Wakefield R.

Range

Throughout the Murray–Darling River system, Bulloo River system, coastal rivers of eastern Australia from Fitzroy River, Qld., south to Clarence River, N.S.W., Hunter River and Nepean–Wollondilly system, N.S.W., coastal rivers of Victoria and South Australia, west to St. Vincent Gulf (Fig. 8).

VELESUNIO LEGRANDI (Petterd)

Plate 2, Figs. 6 and 7

Unio depressus Lamarck, Reeve, 1864, pl. xviii, sp. and fig. 81. (Non *Unio depressus* Lamarck.)

Unio legrandi Petterd, 1889, pp. 81–2.

Unio spp. Johnston, 1889, pp. 95–6, pl. i, figs. 6, 7, 8, 10, pl. ii, figs. 11, 13, 14, 15, 16, 16*a*.

Diplodon australis var. *legrandi* (Petterd) Simpson, 1914, p. 1298. (Non *Unio australis* Lam. 1819.)

Diplodon australis (Lam.) May, 1921, p. 21; 1923, pl. ix, fig. 11. (Non *Unio australis* Lam. 1819.)

Velesunio shuttleworthi (Kuster) Iredale, 1934, pp. 60–1, pl. iii, fig. 5. pl. iv, fig. 5.

Remarks

Iredale (1934) has given an account of the confusion that has existed in the nomenclature of Tasmanian freshwater mussels. After due consideration, he used the name *shuttleworthi* Kuster as the earliest valid name for the Tasmanian *Velesunio*, with *moretonicus* Reeve and *legrandi* Petterd in synonymy. We have been unable to locate the holotypes of either *shuttleworthi* Kuster or *moretonicus* Reeve, both of which were inadequately described and figured, with indefinite localities. Consequently we prefer to set aside both these names as *nomina dubia* and adopt for the present

species the first name definitely given to the Tasmanian *Velesunio*, i.e. *U. legrandi* Petterd, the holotype of which is available. The first definite reference to this species appears to be that of Reeve (1864) who misidentified it as *U. depressus* Lam. Following Petterd's naming of the species, Johnston (1889) attempted to show that all the Australian species were variants of one form, and presented 18 figures of Tasmanian shells to help prove his point. Of these 18 figures, ten, as indicated above, clearly represent *V. legrandi*, while the remaining eight represent *Hyridella* (*Hyridella*) *narracanensis* (Cotton & Gabriel), which also occurs in Tasmania.

Fig. 8.—Distribution of subfamily Velesunioninae. 1, *Velesunio ambiguus*; 2, *V. legrandi*; 3, *V. angasi*; 4, *V. sentaniensis*; 5, *Westralunio carteri*; 6, *W. flyensis*.

D. australis var. *legrandi* Simpson: Simpson's placing of *U. australis* Lam. has been shown above to be incorrect. Hence, his placing of Tasmanian shells as a variety of *australis* is also incorrect. The dimensions given by him indicate *V. legrandi*; no specimen of *H. narracanensis* ever reaches this size.

D. australis (Lam.) May: Following Simpson's (1914) application of *Diplodon* to Australian mussels, May (1921, 1923) listed and figured two species of Tasmanian mussels under that name. The one he called *D. australis* Lam. is clearly *V. legrandi*; the other, regarded by him as "possibly only a variant", is labelled *D. mortonicus* (*sic*) Reeve but is clearly *H. narracanensis*.

Types

U. legrandi Petterd: Holotype AM Reg. No. C. 12905. Type locality: holotype labelled "Sth. Esk R., Tasmania" which must be accepted as restricted type locality.

Description

This species is close to *V. ambiguus* but differs from it consistently in certain characters. Biometrical consideration of shell morphology of the two species further supports their distinction.

Shell Morphology.—Shells of variable size, up to 105 mm long, maximum height up to 65 mm, MHI usually about 62 per cent. Young shells fairly compressed, old shells slightly swollen, never globose. Typical outline ovoid with short anterior end, BLI about 27 per cent. Anterior and posterior margins rounded; dorsal margin posterior to the beaks elevated, BHI usually about 81 per cent., rarely reaching 90 per cent. Ventral margin straight over most of its length, curving evenly to the anterior and posterior margins. Posterior ridge prominent; outline from dorsal aspect almost elliptical, with maximum width in the centre of the hinge.

Periostracum usually dark, even in young shells, showing strong growth lines. Nacre purplish white, showing copper-coloured blotches, usually within the pallial line. Shell always heavy and thick.

Hinge strong, tending to become unionid; lateral teeth moderately long but never thick and rounded, only slightly curved and consistently double in the left valve, the upper tooth shorter and reduced. Cardinal teeth generally large, erect and grooved in young shells, thickened and sometimes reduced in old shells.

Posterior muscle scars well marked, but not deeply impressed, retractor and adductor fused; anterior scars always impressed, usually deep, pitted and roughened in old shells, retractor and adductor fused. Pallial line not prominent.

Anatomy.—With the characters of the genus. Siphons not prominent, branchial up to twice the size anal and bearing 3–4 rows of medium-sized papillae. Palps large, subtriangular, pointing postero-ventrally. Marsupium well developed, occupying middle two-thirds of inner gill in non-gravid females. Both gills subtriangular and deep. Outer gill in both sexes looped, usually with a poorly developed interlamellar junction at each node. Both lamellae have interfilamentar junctions often spanning up to 50 filaments, with thin unfolded walls and numerous thin-walled blood vessels. The ventral margin is rounded. Inner gill of females always with marsupial differentation, thicker than outer gill and not looped. Non-marsupial region with long, thin-walled, heavily vascularized interfilamentar junctions and widely spaced simple interlamellar junctions. In the marsupium, interlamellar junctions well developed, close together, with thick, folded epithelium and pronounced muscle bands crossing between the lamellae. In gills packed with embryos, the marsupium is very swollen, with fewer, thinner interlamellar junctions. Chitinous supporting rods long and heavy at base of filaments.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. legrandi								
Holotype	65	17	26%	45	68%	37	82%	27
Mean of 27 specimens, Brumby Ck., Cressy; ZDQ	78	20	26%	50	63%	40	81%	32

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Mean of 70 specimens, Liffey R., Bishopsbourne; ZDQ	92	27	29%	56	61%	48	86%	36

Material Examined

U. legrandi holotype AM, plus specimens from localities listed below.

Range

May (1923) records "found only in rivers flowing into Bass strait". An examination of these rivers in January 1956 by one of us (I.D.H.) suggested that mussels are confined to the Tamar River system. Kershaw (personal communication) confirms this idea. Localities from which specimens, examined in the present work, have been collected are: South Esk River, Tullochgoroum, Fingal; Lake River, 31 miles from Launceston; St. Paul's River; Liffey River, Bishopsbourne and near Bracknell; Macquarie River, near junction with Elizabeth River, at Campbelltown, Cressy; Blackmann's River, Tunbridge (Fig. 8).

Velesunio wilsonii (Lea)

Plate 2, Figs. 8–11; Plate 3, Figs. 1–3

Unio wilsonii Lea, 1859, p. 113; 1860, p. 256, pl. 40, fig. 137. Sowerby, 1867*a*, pl. 88, sp. and fig. 472. Smith, 1881, p. 311.

Unio (*Alasmodon*) *stuarti* A. Adams & Angas, 1864, p. 417.

Unio stuarti A. Adams & Angas, Sowerby, 1866*a*, pl. liv, sp. and fig. 279; 1867, pl. lv, sp. and fig. 279*a*. Smith, 1881, p. 311. Tate, 1882, p. 55; 1887, p. 101.

Anodon stuarti (A. Adams & Angas) Sowerby, 1870*b*, pl. xxxiv, sp. and fig. 136*a*, 136*b*.

Diplodon bednalli (Tate) Frierson, 1908, p. 118. (Non *Unio bednalli* Tate 1882.)

Diplodon wilsonii (Lea) Simpson, 1914, pp. 1302–3.

Hyridella wilsoni (Lea) Cotton & Gabriel, 1932, pp. 157–8, pl. xvi, fig. 4.

?*Hyridella wilsonii* (Lea) Haas, 1924, p. 75, pl. ii, fig. 3.

Centralhyria stuarti (A. Adams & Angas) Iredale, 1934, pp. 65–6, pl. iii, fig. 12, pl. iv, fig. 12. McMichael, 1952, p. 399.

Centralhyria wilsonii (Lea) Iredale, 1934, p. 66, pl. iii, fig. 13, pl. iv, fig. 13. McMichael, 1952, p. 398.

Centralhyria wilsonii caurina Iredale, 1934, p. 66, pl. iii, fig. 14, pl. iv, fig. 14.

Hyridella anodontaeformis (Tapp. Can.) Johnson, 1948, p. 47. (Non *Microdontia anodontaeformis* Tapp. Can. 1883.)

Velesunio wilsonii (Lea) McMichael, 1956, p. 40.

Remarks

U. wilsonii and *U. stuarti*: The distinction between *U. wilsonii* and *U. stuarti* has always been in doubt, though most authors have regarded them as synonymous. Iredale (1934) attempted to separate them on the grounds that *wilsonii* grew larger and had a thicker shell and persistent teeth in old specimens whereas the teeth of *stuarti* became obsolete. Iredale apparently based his conclusions on large shells from Rockhampton which he regarded as *wilsonii*, whereas they intergrade with *Alathyria pertexta*, which shows the features stressed by Iredale. The holotype of *wilsonii* is a very young shell, from the Isaac's River, a tributary of the Fitzroy River,

north of Rockhampton. The holotype of *stuarti* is a juvenile from a lagoon, near Mt. Margaret, Central Australia. Examination of large series from a wide range of localities has indicated that though variation occurs, there is no constancy in variation which will permit separation of two forms. Shell thickness and tooth development in old shells is quite variable and no evidence can be found to support Iredale's (1934) contention. Haas (1924) recorded specimens under the name *wilsonii* Lea from the Vailala River, Papua, but the figure he gave is certainly not *wilsonii*; it may be *V. sentaniensis* (Haas).

D. bednalli: The shell listed by Frierson (1908) as *Diplodon bednalli* (Tate) is now in the USNM; it is definitely *wilsonii* Lea.

C. wilsonii caurina: Name erected by Iredale for specimens from the May River, north-west Australia, differentiated by a sloping, posterior ventral margin and greater height at the posterior end. One of the many isolated populations of *V. wilsonii* and not legitimately separable subspecifically.

H. anodontaeformis: A specimen recorded by Johnson (1948) from the "Marco River" (= Maro or Merauke River) at Merauke under the name *Hyridella anodontaeformis* is in the MCZ and is undoubtedly *wilsonii*. It is the only non-mainland specimen known and may represent a New Guinea subspecies, but without further material for examination, it is united with typical *wilsonii*.

Types

U. wilsonii Lea: Holotype ANSP No. 41817. Type locality: "Eastern branch of Isaac's Plain, N.S.W."*

U. stuarti A. Adams & Angas: Holotype BM Reg. No. 1870-10-26-40. Type locality: lagoon near Mt. Margaret, Central Australia.

C. wilsonii caurina: Holotype and paratype Reg. No. AM, both C. 42241. Type locality: May River at Meda, north-west Australia.

Description

Shell Morphology.—Shells of varying size up to 125 mm long, maximum height up to 60 mm, MHI usually 46–53 per cent.; shells generally compressed, never globose. Typical outline elongate oval, anterior portion short, BLI usually 25–30 per cent. Anterior margin blunt and evenly rounded; ventral margin slightly rounded in juveniles, straight in older shells; posterior margin generally acuminate, prominently so in some shells; dorsal margin straight and almost parallel to ventral margin, never more than slightly winged, junction with posterior margin obtusely angular.

Periostracum generally smooth and pale olive-green in juveniles changing to dense purple-brown in old shells where growth lines are often prominent; beaks little eroded; nacre bluish white, iridescent; shell substance relatively thin.

Hinge lamellar, weak; lateral teeth long, fine, slightly curved, double in left valve with no marked size difference; cardinal teeth short, delicate, and sharp; all teeth tending to reduction in old shells.

*Isaac's River (= Isaac's Plain) is in central coastal Queensland, not New South Wales, but Queensland was not declared a separate colony until December 10, 1859, hence Lea's apparent error.

Posterior muscle scars fused, very weakly impressed; anterior scars moderately impressed, retractor and adductor fused, protractor prominent and elongate; beak muscle scars numerous, in a row. Pallial line prominent.

Anatomy.—With the characters of the genus; siphons not prominent, lightly pigmented, branchial about $1\frac{1}{4}$ times size anal, bearing 3–4 rows of small papillae. Palps medium-sized, subtriangular to semilunar, pointing posteriorly. Marsupium moderately developed, occupying middle two-thirds of inner gill of females. Outer gill in both sexes tending to loop, but interlamellar junctions not regularly nodal. Interfilamentar junctions long and regular with well-developed walls, occasionally with associated muscle cells. Filaments of inner lamella often long and thin-walled. Ventral margin rounded. Inner gill in females always showing marsupial differentiation, but never prominently developed. Interlamellar junctions regular and long, with thin, unfolded walls and poor muscular development; epithelium often irregularly ciliate; connective tissue never dense. Interfilamentar junctions well developed in non-marsupial section of gill, otherwise irregular and more frequent on outer lamella. Chitinous supporting rods long and thin, at base of ciliated portion of filaments.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. wilsonii Holotype	48	15	31%	25	52%	23	92%	15
U. stuarti Holotype	80	24	30%	37	46%	34	92%	?
C. wilsonii caurina Holotype	74	20	27%	37	50%	34	92%	25
U. stuarti Mean 2 topotypes, Mt. Margaret; NMV	48	15	31%	24	50%	21	88%	12
Maro R. at Merauke; MCZ	85	21	25%	40	47%	33	83%	26

Material Examined

As above, except holotype, plus specimens from SOUTH AUSTRALIA: Lagoons, Mt. Margaret; Macdonnell Downs; Umburn Waterhole, near Mt. Margaret; Algebuckinna; Kopperamanna; South Neil R., Oodnadatta; Innamincka. WESTERN AUSTRALIA: Lennard R.; May R., Meda; Fitzroy R. NORTHERN TERRITORY: Bunday R.; Fraser R.; Goyda Lagoon; Tennant's Ck.; Avon Downs; Port Darwin; Alexandria Downs; Brock's Ck.; Bylang Ck.; Newcastle Waters; Yellow Waterhole; Clifton Hills Station; Daly Waters. QUEENSLAND: Norman R., Karumba; Saxby R., Iffley, Taldora, Millumgara; Flinders R., Hughenden, Sylvania; Cape R., Capeville; Lake Idamea; Eastern Ck.; Julia Ck.; Barron R.; Emmet Downs Station; Pioneer R.; Mary R., Gympie; Murray Lagoons, Rockhampton; Kensington Downs, Greenhills, near Longreach; Barcoo R., Barcaldine; Glenormiston; Cloncurry R., Cloncurry; Carbine Ck., Dajarra; Burdekin R., Macrossan; Jordan R., Jericho; Aramac Ck., Aramac; Thompson R., Muttaburra; Hodgkinson R., Mt. Mulligan; Herbert R., Ingham; Fitzroy R., Paradise Lagoon; Pioneer R., Mackay; Campaspe R.

Range

Mary River, Gympie, Qld., and Queensland coastal rivers from Fitzroy River to Cairns; Norman, Saxby, Flinders, and Cloncurry Rivers to Gulf of Carpentaria;

Lake Eyre drainage system and rivers in north-western Australia and southern New Guinea (Fig. 9).

Fig. 9.—Distribution of subfamily Velesunioninae (*continued*). 1, "*Velesunio ovatus*"; 2, *Microdontia anodontaeformis*; 3, *Velesunio wilsonii*; 4, *Alathyria jacksoni*.

Velesunio angasi (Sowerby)

Plate 3, Figs. 4–12; Plate 4, Figs. 1–6

Unio angasi Sowerby, 1867*a*, pl. lv, sp. and fig. 282. Smith, 1881 (in part), pp. 307–8. Tate, 1882, p. 56; 1889, p. 68.
Anodon angasii Sowerby, 1870*b*, pl. xxxii, sp. and fig. 127.
Unio bednalli Tate, 1882, p. 56.
Centralhyria (*Aparcthyria*) *angasi* (Sowerby) Iredale, 1934, pp. 66–7, pl. v, fig. 4, pl. vi, fig. 1.
Centralhyria bednalli (Tate) Iredale, 1934, p. 67; 1943*a*, p. 190.
Hyridella (*Hyridella*) *bardwelli* Clench, 1934, pp. 89–90, pl. 2, figs. 1–5.
Aparcthyria angasi (Sowerby) Iredale, 1934*a*, p. 190.
Aparcthyria inspecta Iredale, 1943*a*, pp. 191–2.
Aparcthyria hemesa Iredale, 1943*a*, p. 191.
Quaesithyria fleckeri Iredale, 1943*a*, p. 191.

Remarks

Despite Sowerby's accurate figure and the geographic remoteness of the type locality, this species has caused considerable confusion since its description. The main source of confusion has arisen from its erroneous synonymy with species of *Alathyria* which it resembles somewhat in general outline. As shown below, its range is restricted to northern Australia, a region not well known malacologically and poorly represented in most collections. A discussion of the evidence for the present determination of this species and the specific synonymy is warranted.

U. angasi Sowerby: Collected by the Stuart Expedition (1858–62) at Strangway's River, a tributary of the Roper River which flows into the Gulf of Carpentaria. The holotype, in the British Museum, was described and figured by Sowerby, the figure showing concentric ridges on the beaks (though the description reads "Umboes smooth, sub-depressed") but otherwise fairly accurate. Smith (1881) synonymized *angasi* with *shuttleworthi* Lea, but noted that the name *shuttleworthi* was preoccupied by Kuster (1855) and used *angasi* as the best available name. Smith, however, listed the Balonne River, Brisbane River, and Isaacs River, as well as Strangway's River, as localities for *angasi*, and thus initiated much subsequent confusion. Tate (1882) listed *angasi*, but gave only the type locality, which suggests that he had no specimens of his own. The same author later (1889) listed *angasi* again, but incorporated Smith's error in his comments. More recently, Cotton and Gabriel (1932) have used *angasi* in Smith's sense, i.e. applied the name to true *angasi* (by reference to type locality) and to *Alathyria* spp. from Queensland, New South Wales, and Victoria. Their figured specimen (pl. xvi, fig. 3) has been examined and is clearly *Alathyria jacksoni* Iredale. Gabriel (1939), repeating his and Cotton's earlier error, applied the name to and figured the same specimen of *A. jacksoni* from Cramenton, Vic. Frierson (1908) concluded that *angasi* Sowerby did not equal *shuttleworthi* Lea, and Iredale (1934) confirmed this, realizing that Sowerby's *angasi* could not be an *Alathyria* and commented that it "is easily recognized when Northern Territory shells are examined". Iredale's introduction of *Aparcthyria* for the species has been discussed above.

A. angasii Sowerby: Two specimens in the BM are labelled as such. The tablet to which they are affixed bears the label "Burke R.". Both specimens are *V. angasi*.

U. bednalli Tate: Name given to shells from the Adelaide River and from Yam Creek, Glencoe. Tate compared this species with *U. stuarti* A. Adams & Angas (= *V. wilsonii* (Lea)) from which it differed "in being more tumid, less inequilateral and in its truncated, not acuminate, posterior margin". Colour differences in the periostracum were also noted. The holotype is definitely *angasi*, though a little less winged and more elongate. In the same paper, Tate also listed *angasi* Reeve (= Sowerby) by type locality only and *Unio* (aff.) *angasi* from ponds near the Adelaide River and from tributaries of the McKinlay River. These localities are all close together and the shells examined by Tate are in the South Australian Museum. Though they differ slightly among themselves, they are considered as merely ecophenotypes of true *angasi*. Frierson (1908) considered *bednalli* to be close to *wilsonii* Lea. His specimen, now in the USNM, is in fact *wilsonii*, not the present species.

H. (*Hyridella*) *bardwelli* Clench: Unaware of Iredale's (1934) paper, Clench described *bardwelli* from the Glenelg River in northern Western Australia. It was compared with *U. wilsonii* Lea from which it differed in being smaller, more winged, and of relatively greater height and thickness. Clench placed the species in *Hyridella*, following Thiele's (1934) modification of Cotton and Gabriel's (1932) generic arrangement. The type is identical with *Aparcthyria inspecta* Iredale.

A. inspecta Iredale: Name given to a series of shells from creeks and ponds around Darwin. They all showed more pronounced winging than *angasi*, and though the shells from each locality showed slight differences, Iredale regarded them as

"all merely ecologic variations of the one species". We regard them as variants of *V. angasi*.

A. hemesa Iredale: Applied to shells from Wenlock Downs, Batavia River, which flows into the Gulf of Carpentaria, Queensland. They differ from typical *angasi* by being smaller, more swollen, and having a more pronounced anterior end. They match the description of *U.* (aff.) *angasi* by Tate (1882) and compare with specimens from the McKinlay River in the SAM, probably collected by Tate. We do not regard them as separable from *angasi*.

Q. fleckeri Iredale: Name for shells from the Hodgkinson River, North Queensland, believed by Iredale to be smaller relatives of *Quaesithyria* (= *Alathyria*) *wardi* Iredale, but inspection of the type material shows that they belong here and not with *Alathyria*.

All the forms described above have one common attribute, in that they show some degree of winging. They are closer to *wilsonii* Lea than other species in the genus, but differ from it consistently in being more tumid and always truncate, never acuminate, posteriorly. Examination of a series of shells from Cape York across northern Australia to the Kimberley region suggests that there are no grounds for regarding these different forms as anything beyond ecophenotypes of *angasi* Sowerby.

Types

U. angasi Sowerby: Holotype BM Reg. No. 1870-10-26-41. Type locality: Strangway's R., North Australia.

U. bednalli Tate: Holotype SAM Reg. No. D. 14427 is labelled (in Verco's handwriting) "*Diplodon bednalli* Tate. Tate's collection, probably his type". Another label repeats this and adds "N.T. River Adelaide, at the ford—HOLOTYPE". The dimensions are almost the same as those given by Tate (1882) (see "*Dimensions*" below). This specimen is very probably the holotype. Paratypes SAM Reg. No. D. 13999, five pairs and one single valve labelled "Yam Ck., Glencoe. Tate Collection".

H. bardwelli Clench: Holotype MCZ Reg. No. 41999. Type locality: Glenelg R., northern Western Australia. Paratypes MCZ, Reg. No. 42000, AM Reg. No. C. 61729, SAM Reg. No. D. 14015; MZUM ?

A. inspecta Iredale: Holotype AM Reg. No. C. 61637. Type locality: Holmes Creek, 12 miles NE. of Darwin, N.T. Paratypes AM Reg. No. C. 61638, MCZ Reg. No. 196597. Paratypes from nearby localities (Iredale 1943*a*) are in AM Reg. Nos. C. 61639, C. 61640, C. 61641.

A. hemesa Iredale: Holotype AM Reg. No. C. 61739. Type locality: Wenlock Downs, Batavia R., Qld. Paratypes AM Reg. No. C. 61883.

Q. fleckeri Iredale: Syntypes AM Reg. No. C. 61722. Lectotype, here selected, is specimen whose dimensions were given by Iredale and is here figured. Type locality: Hodgkinson R., north Queensland.

Description

Shell Morphology.—Shells of variable, but never large, size, up to about 90 mm in length and 45 mm high, MHI of the order of 50–60 per cent.; usually compressed, never globose. Shells elongate oval, expanded posteriorly; anterior portion short, BLI about 25 per cent. Anterior margin slightly truncate dorsally, then uniformly rounded; ventral margin straight or rarely convex or slightly sinuate; posterior margin uniformly rounded ventrally, then running straight up to dorsal margin to form a wing; dorsal margin straight but depressed anteriorly, straight posteriorly and elevated to a varying degree, usually sufficiently to produce a pronounced wing,

BHI about 80 per cent. Posterior ridge usually prominent, but rounded; beaks often elevated, always smooth, usually only slightly eroded.

Periostracum dark brown to black, marked with moderately strong, fairly regular, growth lines. Nacre typically bright, grey-blue, sometimes iridescent, with a deep copper blotch, mottled with yellow, in the region of the beaks; usually with fine striations radiating from the beaks. Shell substance always thin.

Hinge lamellar, moderately strong; lateral teeth fairly long, only slightly curved, double in left valve (though sometimes single, e.g. holotype *U. bednalli* Tate); cardinal teeth low, long, and sharp, especially single, left tooth.

Muscle scars weakly impressed; posterior retractor and adductor fused, almost invisible; anterior retractor and adductor fused, protractor moderately elongate; beak muscle scars few, in a row. Pallial line weakly impressed.

Anatomy.—With the characters of the genus. Siphons brick-red with black blotches (pigment extending to the postero-ventral border of mantle) not prominent; branchial about $1\frac{1}{2}$ times size anal, bearing a single row of pale papillae. Palps sub-triangular heavily ridged on the opposing faces. Marsupium prominent in females, but small, occupying the middle half of the inner gills. Outer gill in both sexes with irregular loops and interlamellar junctions; interfilamentar junctions long, with thick epithelium and well vascularized. Inner gill of females always with marsupial differentiation, never looped; non-marsupial portion same as outer gill; marsupium with numerous interlamellar junctions, many short and incomplete, with thick, folded epithelium, cells occasionally ciliate, musculature well developed, connective tissue dense; interfilamentar junctions well developed, especially on outer face, being almost continuous along inner lamella. Chitinous supporting rods long and heavy, at base of filaments.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. angasi Sowerby								
Holotype	75	20	27%	41	55%	34	83%	?
A. angasii Sowerby								
Mean 2 specimens; BM	70	16	23%	39	56%	32	82%	23
U. bednalli Tate								
Tate's data	79	23	29%	40	51%	?	?	30
Recent measurements	77	18	23%	40	52%	32	80%	32
H. bardwelli Clench								
Holotype	54	12	22%	31	57%	25	81%	20
H. bardwelli								
Mean 4 paratypes	52	11	21%	28	54%	23	82%	19
A. inspecta Iredale								
Holotype	75	19	25%	43	57%	37	86%	25
A. inspecta								
Mean 5 paratypes; AM	52	11	21%	31	59%	25	81%	19
A. hemesa Iredale								
Holotype	56	13	23%	33	59%	29	88%	22

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
A. hemesa								
Mean 5 paratypes;								
AM	46	11	24%	28	60%	23	82%	16
Q. fleckeri Iredale								
Type	92	17	18%	46	50%	38	83%	28
V. angasi								
Mean 4 specimens,								
Roper R.; ZDQ	65	15	23%	36	55%	28	78%	21

Material Examined

Types as above and specimens from WESTERN AUSTRALIA: Glenelg R.; Forrest R.; Lennard R.; Wittenoom Gorge; Barton R.; Adelaide R. NORTHERN TERRITORY: Lake Dean, Holme's Ck., Banker's Jungle Ck., Howard Ck. (all near Darwin); Port Darwin; Red Lilly Lagoon; McKinlay R.; Roper R., Leichardt's Bar; Fitzmaurice R.; Strangway's R.; Katharine R., Mambulloo; Yam Ck., Glencoe; Connexion Island. QUEENSLAND: Palmer R., Palmerville; Batavia R., Wenlock Downs; Silver Valley; Hodgkinson R.; Gilbert R.; Norman R.; Gregory R., Riversleigh; Claudie R.

Range

In coastal streams and lagoons of northern Australia, from the west coast of Cape York to the Lennard River, northern Western Australia (Fig. 8).

VELESUNIO SENTANIENSIS (Haas)

Plate 4, Figs. 7–10

Hyridella sentaniensis Haas, 1924, pp. 72–4, text figs. 4–12, pl. ii, fig. 6. Jutting, 1935, pp. 73–4, text figs. 3–10.

Unio beauforti Bavay, 1908 (in part), p. 291.

Velesunio sentaniensis (Haas) McMichael, 1956, p. 39.

Remarks

U. beauforti was described from specimens collected in Lake Sentani and Lake Jamur, Dutch New Guinea. The type was stated to have come from the former locality, but Haas (1924), on the authority of the collector, de Beaufort, gave Lake Jamur as the true locality. Haas (loc. cit.) placed *U. beauforti* as a synonym of *Microdontia anodontaeformis* Tapp. Can., but gave some of the paratypes from Lake Sentani a new name, *Hyridella sentaniensis*. These differed from *U. beauforti* in being smaller, with a weak lamellar hinge. We have seen no specimens comparable to the holotype of *U. beauforti* and so cannot comment on Haas's separation of *sentaniensis*, but several series of shells, including topotypes, of the latter have been examined. Under the circumstances, Haas's arrangement has been followed.

Haas placed *sentaniensis* in *Hyridella* on the basis of its close relationship to *H. australis* (Lam.) as described by Ortmann (1912). As outlined above, Ortmann's specimens were *V. ambiguus* (Phil.), and the present species is clearly a *Velesunio*.

Types

Holotype and paratypes of *H. sentaniensis* are in the Zoological Museum, Amsterdam, and a paratype is in the Australian Museum. Holotype from Lake Sentani, south of Hollandia, Dutch New Guinea. Most paratypes from same locality, one small fragment from Moaif, west of Hollandia. The holotype is figured by Haas (1924), pl. ii, fig. 6.

Description

Shell Morphology.—Shells of relatively small size, up to 50 mm long, MHI usually 55–60 per cent.; shells a little swollen, never globose. Typical outline elongate ellipse, anterior end relatively short, BLI about 25 per cent. Anterior margin usually evenly rounded, sometimes truncate; ventral margin straight and prolonged, sometimes with a noticeable sinuation posteriorly; posterior margin rounded, but deflected ventrally; dorsal margin slightly curved, slightly elevated posteriorly, BHI about 83 per cent.

Periostracum browny black, straw-coloured in juveniles, silky; growth lines very lightly marked; nacre bluish white, never blotched; shell substance thin.

Hinge weak; lateral teeth short, slightly curved, relatively thick, usually double in left valve, sometimes in right, sometimes single in both valves; cardinal teeth prominent, thin, sharp, immediately dorsal to anterior retractor muscle.

Muscle scars very lightly impressed, posterior retractor and adductor scars fused, protractor scar tongue-shaped; beak muscle scars 3–5, scattered. Pallial line weakly impressed.

Anatomy.—With the characters of the genus; siphons not prominent; anal usually red-brown with black blotches; branchial about 1½ times size anal, well demarcated from mantle edge, more deeply pigmented (pigment extending well around ventral mantle margin), bearing 2 rows of medium-sized, pale papillae. Palps small, subtriangular, pointing posteriorly. Marsupium well developed, occupying middle two-thirds of inner gill. Outer gill in both sexes not looped; interlamellar junctions few and irregularly spaced; interfilamentar junctions long with simple, thin epithelium. Inner gill in male and in female, non-marsupial section, as above; in marsupium, interlamellar junctions numerous, close-packed, walls of middle section folded, epithelium simple, irregularly ciliate, muscles weakly developed, connective tissue sparse. Chitinous rods small, fat in section, at base of filaments.

Glochidium.—Unknown here or Haas (1924).

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype from Haas (1924) and fig.	48	12	25%	26	55%	22	85%	17
Specimens ex Jutting (1935)	40	10	25%	22	55%	19	86%	?
Mean 3 topotypes; MZUM	41	10	25%	23	56%	20	87%	14
Mean 35 specimens Lae, N.G.; AM	40	10	25%	24	60%	20	83%	14
Mean 16 topotypes; AM	41	10	25%	23	57%	19	83%	14

Material Examined

As above and from Hollandia, Dutch New Guinea; Aitape, Territory of New Guinea; tributary of Ramu R., Aiome, Territory of New Guinea.

Range

North coast of New Guinea (Fig. 8).

Nomina Dubia

Unio shuttleworthi Kuster, 1855, pl. 44, fig. 2; 1856, p. 152. Smith, 1881, p. 311.

Remarks

Kuster gave the type locality as "Neuholland" but the description and figure are inadequate for determining whether this is a mainland or Tasmanian shell. As indicated above, Iredale (1934) accepted the name for the Tasmanian *Velesunio*, but, without access to the holotype, we prefer to regard the species as unidentifiable. Modell (personal communication) suggests that the type was probably in Leipzig and destroyed during World War II.

Unio moretonicus Reeve, 1865, pl. xxiv, sp. and fig. 118.

Remarks

Reeve gave "Tasmania and Moreton Bay, Australia" as type locality. His figure and description are totally inadequate and the present authors know of no population from either locality or any other Australian locality with which it can be identified. The figure is probably of a *Velesunio*. While a number of authors, including Tenison-Woods (1875) and Johnston (1879), accepted the Tasmanian locality and used the name for the Tasmanian *Velesunio*, they were aware of the inconsistency of the localities given by Reeve. The holotype cannot be located in the British Museum; until it can be studied, this species cannot be determined.

Genus MICRODONTIA Tapparone Canefri

Microdontia Tapparone Canefri, 1883, p. 295. Type species by monotypy: *Unio anodontaeformis* Tapparone Canefri 1883.

Remarks

The genus was originally proposed as a section of *Unio* by Tapparone Canefri. The name was not used by Simpson (1900) who placed the species for which it was erected in a large heterogeneous group, *Nodularia* Conrad. Haas (1910) accepted *Microdontia* and added a second species, *M. ovata* Haas. That species is here regarded as a doubtful species in the Australian genus *Velesunio* Iredale.* Haas (1913) retained *Microdontia* for the same two species and gave a fairly detailed generic analysis. At the same time he suggested a relationship with Australian species placed in *Diplodon*. Simpson (1914) retained his original opinion and grouped both species under *Nodularia*. Haas (1924) relegated *Microdontia* to the synonymy of the Australian genus "*Hyridella*" (= *Velesunio* Iredale) on the basis of the resemblance of *M. ovata* and juvenile, non-rostrate *M. anodontaeformis* to *Velesunio*. While this action may have been correct with reference to *ovata*, which may belong in *Velesunio*, *anodontaeformis* differs sufficiently from Australian velesunionine mussels to be separated generically from them. In many respects *Microdontia* recalls *Alathyria* but may not be closely related to it. As yet, the genus is monotypic.

Diagnosis

Shell Morphology.—Large shells of almost anodontine facies of the subfamily Velesunioninae. Shells swollen, posterior end produced ventrally as a rostrum. Hinge

*See p. 481.

unionid with elongate lateral and grooved cardinal teeth. Anterior muscle scars deeply impressed; retractor and adductor scars fused. Periostracum usually smooth.

Anatomy.—Unknown.

Glochidium.—Unknown.

Distribution

South coast rivers of New Guinea and also (?) Sepik River.

Relationships

The nearest relatives to *Microdontia* appear to be the Australian Velesunioninae, particularly *Velesunio* and *Alathyria*. It can be distinguished from the former by its size and strong hinge and from the latter by its characteristic rostration. Fossils belonging to this genus are unknown.

Microdontia anodontaeformis Tapparone Canefri
Plate 4, Figs. 11 and 12

Unio (*Microdontia*) *anodontaeformis* Tapparone Canefri, 1883, pp. 295–6, pl. ii, figs. 3–5.
?*Unio beauforti* Bavay, 1908 (in part), p. 291, pl. 14, fig. 16.
Microdontia anodontaeformis Tapp. Can., Haas, 1913, p. 162, pl. 16, fig. 6. McMichael, 1956, p. 41.
Nodularia anodontaeformis (Tapp. Can.), Simpson, 1914, p. 1010.
Hyridella anodontaeformis (Tapp. Can.), Haas, 1924, pp. 69–71, pl. 2, figs. 1 and 2.

Remarks

The shells from the Fly and other southern New Guinea rivers described under this name are quite distinct from all other Australasian species. Though their generic placement has been in doubt, as discussed above, no author has doubted their specific distinctness. There is one doubtful synonym, *Unio beauforti* Bavay, and the reason for the doubt warrants discussion.

Haas (1924) first placed *U. beauforti* in the synonymy of *M. anodontaeformis*, after examining three lots of specimens, viz. the type series of *anodontaeformis*, the type series of *beauforti*, and some *anodontaeformis* from the Vailala River, south-eastern New Guinea. While the latter series appear to be *anodontaeformis*, the lack of rostration in young shells caused Haas to place the species in "*Hyridella*" (= *Velesunio* Iredale). The growth lines of Fly River specimens of this species indicate that rostration appears early, but Haas believed it to be an ecophenotypical character induced by environment. While this view may be correct, it remains a fact that no Australian shell shows this character to any extent. Further, other structural differences, particularly in the hinge, warrant generic separation of this species from the genus *Velesunio*.

The types of *U. beauforti* were from Lake Jamur and Lake Sentani in Dutch New Guinea. Bavay (1908) stated that the holotype was from Lake Sentani, but Haas (1924) reports that de Beaufort, the collector, had informed him that it was from Lake Jamur. The specimens from Lake Sentani were renamed *Hyridella sentaniensis* by Haas. The holotype of *beauforti* from Lake Jamur approached *anodontaeformis* in size but lacked the rostration and differed in other features. Haas again considered the differences to be ecophenotypic. All the *anodontaeformis*

examined in the present work have been remarkably constant in form, but we have been unable to examine any "*beauforti*" forms and are forced to accept the synonymy as it stands, with reservation. The figure of *Unio beauforti* suggests that it belongs with the Australian genus *Alathyria*, but under the present circumstances the problem remains an open one (see under *Alathyria pertexta magnifica*, below).

Types

The holotype of *M. anodontaeformis*, according to Haas (1924), is in the Museo Civico di Storia Naturale, Genoa, Italy. Haas stated that Tapparone Canefri (1883) figured a paratype and not the holotype of this species, and so figured the holotype himself (pl. 2, fig. 1). Type locality: Fly R., Territory of New Guinea.

The types of *U. beauforti* are in the Zoological Museum, Amsterdam (fide Schepman, 1919). Type locality: Lake Jamur, Dutch New Guinea.

Description

Shell Morphology.—Shells large, maximum length about 130 mm, MHI about 55 per cent. Anterior portion of shell relatively short, BLI about 22 per cent. Anterior margin bluntly rounded; ventral margin gently rounded, slightly sinuate posteriorly; dorsal margin posterior to beaks slightly elevated, BHI 86 per cent., slightly curved, then obliquely truncate; posterior margin extended, forming a bluntly angulate rostrum. Shells swollen, posterior slope compressed, posterior ridge fairly prominent continuing out to the rostrum. Beaks elevated, swollen, unsculptured.

Periostracum olive to dark brown, smooth in juveniles, slightly corrugated in older shells. Nacre whitish iridescent, copper-stained posteriorly. Shell substance strong, fairly thick.

Hinge strong; lateral teeth long, double in left, single in right valve; cardinals heavy, grooved, one main and one accessory in each valve.

Anterior muscle scars firmly impressed, retractor and adductor fused, but retractor posterior, not dorsal, to adductor; posterior scars lightly impressed. Beak muscle scars few and irregular. Pallial line prominent, especially anteriorly, slightly crenulate.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
M. anodontaeformis								
Holotype, ex Haas	129	30	23%	66	51%	57	86%	45
Paratype ex Tapp. Can.	95	28	29%	52	55%	46	88%	?
U. beauforti								
Holotype, ex Bavay	70	17	24%	37	53%	32	86%	20
M. anodontaeformis								
Fly R.; AM	125	26	21%	65	52%	54	83%	42
Sepik R. Juvenile; AM	55	13	24%	33	60%	30	90%	19

Material Examined

As above, excluding types, and from Kikori R., Middletown, Papua; Digoel R., Tanah Merah, Dutch New Guinea.

Range

South coast of New Guinea from Vailala River to Fly River and (?) Lake Jamur, Dutch New Guinea; and (?) Sepik River, Territory of New Guinea (Fig. 9).

Genus ALATHYRIA Iredale

Alathyria Iredale, 1934, p. 63. Type species by original designation: *Alathyria jacksoni* Iredale, 1934.

Quaesithyria Iredale, 1943*a*, p. 191. Type species by original designation: *Quaesithyria wardi* Iredale, 1943*a*.

Remarks

This genus of the subfamily Velesunioninae was erected to accommodate a number of species characterized by their large size, heavy shell, oval outline, and strong unionid hinge. Next to *Velesunio*, it is the most widespread and abundant genus in Australasia, and like it is confined to Australia and New Guinea.

Prior to Iredale's (1934) revision of Australian mussels, the forms included in this genus were assigned to either *Unio shuttleworthi* Lea, which was preoccupied, or *Unio angasi* Sowerby which is a *Velesunio*. Some specimens were even labelled "*Hyridella australis*", a name which at times was the dumping ground for most Australian mussels.

The group as defined by Iredale and largely accepted here is a well-defined one. The generic name *Quaesithyria* was proposed for a northern Queensland species (*Alathyria pertexta wardi*) which possessed a weaker hinge. The species is a typical *Alathyria*, very closely related to *A. pertexta*, and the generic name is not admitted here. A second species, described as *Quaesithyria fleckeri* has been placed in the synonymy of *Velesunio angasi* Sowerby.

Diagnosis

Shell Morphology.—Freshwater mussels of the subfamily Velesunioninae of large size, reaching a maximum length of 160 mm. Shell outline elongate oval, rounded or winged posteriorly as adults, always winged as juveniles, MHI 50–65 per cent. Hinge weak to strong, typically unionid; cardinal teeth heavy, erect and denticulate, sometimes reduced to low ridges in old shells; lateral teeth prominent in juveniles, usually reduced and shortened in adults. Beaks always smooth; shells moderately to strongly swollen; shell substance typically thick, especially at the antero-ventral border, reaching 10 mm or more. Muscle scars heavily impressed, anterior adductor and retractor fused, retractor often a deep pit below the cardinal tooth; posterior scars often comparatively light. Pallial line always prominent, often crenate.

Anatomy.—Supra-anal opening absent, siphons large but not protruding, branchial 1½–2 times size anal, bearing 2–3 rows papillae internally, open below. Siphons separated by prominent mantle bridge and whole area deeply pigmented. Labial palps very large, semilunar. Outer lamellae of outer gills completely fused to mantle; inner lamellae of inner gills fused to visceral mass and united behind it forming a diaphragm which unites with the mantle bridge; diaphragm moderately long and perforate at its junction with mantle bridge.

Outer gills subtriangular and free at edges except on dorsal border; internally with weakly developed interlamellar junctions. Inner gills fused dorsally and anteriorly to visceral mass and partly fused anteriorly to dorsal border of palps near their junction with mantle and visceral mass; internally simple in male, always exhibiting marsupial development in female in at least three-fourths of gill, usually anteriorly placed. Interlamellar junctions in marsupium close together, showing moderate muscle development; frequently reduced to discontinuous septa, invariably so in fully gravid gill (Plate 18, Figs. 1 and 2).

Glochidium.—Subtriangular, hooked (Figs. 10 and 11).

Distribution

Queensland coastal streams, coastal streams of N.S.W. south to the Shoalhaven; Murray–Darling system but rare in Victorian tributaries of Murray River; rare in Lake Eyre drainage; Bian River, Dutch New Guinea.

Differential Diagnosis of Species

Four species and two subspecies are admitted in this genus. *A. pertexta pertexta* is characteristically elongate, MHI 50–55 per cent., has the dorsal margin excavate anterior to the beaks, reduced hinge teeth, and a characteristic purple nacre. *A. pertexta wardi* is elongate, usually less so than *A. p. pertexta*, has MHI 55 per cent., whitish nacre and a marked sinuation in the ventral border of the shell, posteriorly, and also has a weak hinge. *A. pertexta magnifica*, subsp. nov., from New Guinea, reaches a very large size, is very elongate, and has MHI of 43 per cent. *A. jacksoni* is more oval, MHI 55–60 per cent., always winged and rarely has reduced teeth. *A. profuga* and *A. condola* are rounded forms, *A. condola* especially so, MHI 65 per cent. They are distinguished by the excessively rounded and swollen shell, lack of winging and strong teeth in *A. condola*, whilst *A. profuga* is a little more elongate, winged, and has a reduced hinge.

Relationships

The genus *Alathyria* may be distinguished from other members of the subfamily by its large size, thick shell, and usually strong hinge. It is closely related anatomically, in the larval stage, and in its chromosome number to *Velesunio*. *Westralunio* has a strong hinge, but is never large and never winged. The New Guinea genus *Microdontia* approaches *Alathyria* in size but has a thinner shell and a markedly rostrate posterior end. A possible relationship between *Alathyria* and *Haasodonta* is discussed below.

The occurrence of a fossil, *Alathyria tamarensis* (Etheridge Jr.), in the Eocene beds of the Launceston Basin in Tasmania is interesting since the genus is not represented there at the present time.

Alathyria jacksoni Iredale

Plate 5, Figs. 1–5

Unio angasi Sowerby, Smith, 1881 (in part), p. 307. (Non *Unio angasi* Sowerby, 1867*a*.)

Hyridella angasi ("Reeve") Cotton & Gabriel, 1932 (in part), p. 157, pl. xvi, fig. 3; Gabriel, 1939, p. 130, pl. iv, fig. 39.

Alathyria jacksoni Iredale, 1934, pp. 64–5, pl. iii, fig. 11, pl. iv, fig. 11; McMichael 1952, p. 398; Kershaw, 1956, p. 53.

Alathyria jacksoni alleni Iredale, 1943*b*, p. 89.

Alathyria selwyni Iredale, 1943*b*, p. 89.

Remarks

The usage of *Unio angasi* Sowerby 1867 by Smith (1881) refers only in part to the present species. Smith included the true *Velesunio angasi* (Sowerby) from northern Australia, the present species (Balonne River), and *Alathyria pertexta* Iredale (Brisbane and Isaac's Rivers), the latter also by synonymy with *Unio shuttleworthi* Lea. Cotton and Gabriel's (1932) use of *angasi* refers in part to the present species, by locality and figure, and in part also to true *Velesunio angasi*, and to *Alathyria profuga* (Gould), the latter two by locality reference. Gabriel (1939) used *angasi* for the present species, his figured specimen (pl. iv, fig. 39) from Cramenton, Vic., being quite definitely *A. jacksoni*.

Iredale (1934) correctly identified a Northern Territory species as *Unio angasi* Sowerby 1867, and gave a new name to the present species, based on specimens from the Barwon River, New South Wales. In a later paper (1943*b*), he named a new subspecies, *A. jacksoni alleni* from the Macquarie River, and a new species, *A selwyni* from Leeton, Murrumbidgee River. Examination of a large series of shells from throughout the Murray–Darling River system shows shells similar to both, intergrading with typical *jacksoni*. Neither subspecific nor specific separation are warranted.

Types

A. jacksoni Iredale: Holotype AM Reg. No. C. 33006. Paratypes C. 61772. Type locality: Barwon R., N.S.W.

A. jacksoni alleni Iredale: Holotype AM Reg. No. C. 61744. Paratypes C. 61745. Type locality: Macquarie R., Dubbo, N.S.W.

A. selwyni Iredale: Holotype AM Reg. No. C. 61764. Paratypes C. 61888. Type locality: Murrumbidgee R., Leeton, N.S.W.

Description

Shell Morphology.—Adult shells large, reaching about 150 mm in length, MHI 55–60 per cent. Outline almost oval, the anterior end the narrower. Anterior portion of shell short to moderately developed, BLI 20–25 per cent. Anterior margin evenly rounded; ventral margin gently curved; dorsal margin almost straight in young, gently curved in older shells, sometimes very slightly excavated anterior to the beaks; behind the beaks the dorsal margin is elevated, BHI about 80 per cent.; in young shells it is abruptly and obliquely truncate posteriorly, the shell appearing distinctly winged, but in old shells the truncation is less abrupt and the winging less apparent; posterior margin, ventrally, is evenly rounded.

Periostracum olive-brown in young shells, brown-black in old, growth lines very fine in young shells, prominent in old. Nacre distinctly bluish and unstained in young shells, white and with copper-coloured blotches, particularly below the beaks, in adults. Shell substance very thick in large shells, especially near the antero-ventral border where it may reach 10 mm or more. (The shells alone of a specimen 156 mm long weigh 255 g.)

Shells moderately swollen, posterior ridge slightly inflated, beaks not swollen, smooth, but little elevated. Hinge moderately strong, with strong, curved, lateral teeth tending to fuse anteriorly, but always erect and sharp posteriorly; cardinals heavy and thick, grooved and serrated in young shells, sometimes smoothing,

sometimes persisting, the teeth appearing as jagged crags, and sometimes reduced to low ridges in old shells.

Anterior muscle scars deeply impressed, retractor forming a deep pit under the cardinal teeth and fused to adductor scar, protractor scar deep and tongue-shaped. Posterior scars lightly impressed; beak muscle scars variable but usually deep in old shells. Pallial line deeply impressed, often crenulate.

Anatomy.—With the characters of the genus. Anal siphon large but not protruding; branchial 1½–2 times size anal and bearing 2–3 rows of medium sized papillae; siphonal area evenly and usually deeply pigmented. Palps large and semi-lunar in shape.

Outer gill in both sexes regularly looped with regularly spaced interlamellar junctions occurring about every 16–18 filaments, the junctions bearing folded epithelium and a trace of musculature. Interfilamentar junctions extensive with large blood spaces, thus constricting the water-tubes in the gill.

Inner gill of female same as outer gill at lateral extremities. Marsupium occupies middle three-quarters of gill; interlamellar junctions closely packed, with large mucus cells at their inner end, otherwise connective tissue dense and epithelium thick, folded, and usually ciliate; muscle bands in the junctions very prominent. The junctions are mostly discontinuous and originate equally from either inner or outer lamella.

Chitinous supporting rods very wide, at the base of the filaments. Lateral cilia on filaments very long.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
A. jacksoni Holotype	105	20	16%	62	59%	50	81%	37
A. selwyni Holotype	102	22	24%	56	53%	47	84%	36
A. selwyni Paratype	105	23	22%	58	55%	46	79%	35
A. jacksoni alleni Holotype	150	32	23%	87	59%	73	84%	61
Mean 2 specimens; Murray Bridge, S.A.; MCZ	84	20	24%	46	55%	38	83%	27
Mean 12 specimens; Murray R., Vic.; NMV	90	22	24%	49	54%	39	80%	30
Mean 9 specimens; Condamine R., Cecil Plains, Qld.; ZDQ	101	25	25%	59	58%	47	80%	32
Mean 4 specimens; Balonne R., Bindle, Qld.; ZDQ	60	14	23%	33	55%	26	79%	15

Material Examined

As above and from QUEENSLAND: Thomson R., Muttaburra; Barcoo R., Blackall, Barcaldine; Dumaresque R., Texas; Condamine R., Springvale, Cecil Plains; Balonne R., Bindle; Dalby Ck. NEW SOUTH WALES: Bogan R.; McIntyre R., Boggabilla; Macquarie R., Dubbo, Trangie, Bathurst; Barwon R., Brewarrina, Collarenebri, Wàlgett; Lachlin R., Condobolin; Murrumbidgee R., Narrandera, Yanco, Leeton; Darling R., Bourke, Kallard South; Murray–Darling junction; Lake Tairs; Namoi R., Narrabri. VICTORIA: Mitchell R., Bairnsdale; Murray R., Merbein, Echuca, Cramenton; Goulburn R., Arcadia; Saltwater R., Keilor. SOUTH AUSTRALIA: Lake Bonney; Murray R., Moorook, Berri, Swan Reach, Devon Downs, Morgan, Mannum, Murray Bridge, Tailem Bend.

Range

Throughout the Murray–Darling River system and its tributaries (Fig. 9).

ALATHYRIA PERTEXTA PERTEXTA Iredale

Plate 6, Figs. 1–4; Plate 18, Figs. 1 and 2

Unio shuttleworthi Lea, 1856, p. 94; 1857, p. 304, pl. 28, fig. 19. Sowerby, 1866*a*, pl. 32, sp. and fig. 167. (Non *Unio shuttleworthi* Kuster, 1855, pl. 44, fig. 2.)

Unio angasi Sowerby, Smith, 1881, p. 307 (in part). (Non *U. angasi* Sowerby, 1867*a*, nor *Anodon angasii* Sowerby, 1870*b*.)

Alathyria pertexta Iredale, 1934, p. 64, pl. iii, fig. 10, pl. iv, fig. 10.

Centralhyria wilsonii (Lea), Iredale, 1934, p. 66 (in part), pl. iii, fig. 13, pl. iv, fig. 13 (specimens from Gladstone and Mary River, Queensland). (Non *Unio wilsonii* Lea, 1859.)

Alathyria morti Iredale, 1943*b*, p. 89.

Remarks

Examination of the holotype of *U. shuttleworthi* Lea in USNM reveals that Iredale (1934) was correct in assuming it to be a Queensland coastal species. Lea gave only "Australia" as type locality but "Moreton Bay" is pencilled on the inside of the shell. Moreton Bay was the name used for the settlement on the Queensland coast in the vicinity of Brisbane, and Lea's specimen could well have come from the Brisbane River, shells from this locality resembling it very closely. Iredale (1934), however, seems to have misunderstood the species, regarding some less winged forms, with reduced teeth, from mid-coastal Queensland as outsized *Velesunio wilsonii* (Lea) and believing that only the more winged southern coastal form was *U. shuttleworthi* Lea. Since the name was preoccupied, a new name *Alathyria pertexta* was given and a new holotype selected.

Examination of a large series of shells from the coastal rivers from northern New South Wales to the Fitzroy River, Queensland, as well as some inland forms, has revealed that *A. pertexta* is a very variable species in its adult form, ranging from the winged, narrower southern form to a rounded, swollen form typical of swamps and lagoons. The elongate, less winged form, regarded as *V. wilsonii* by Iredale, is typical from mid-coastal Queensland, but is easily distinguishable from true *wilsonii* which often occurs with it. There is complete intergrading between the adult forms of *pertexta* and, more important, the juveniles, irrespective of adult form, are identical. The shell named *A. morti* by Iredale (1943*b*) from the Richmond River, is a particularly elongate form, but cannot be separated specifically from *A. pertexta* on the basis of one isolated ecophenotypic population.

Unio shuttleworthi Lea has been confused considerably in the past. Smith (1881) used the name *Unio angasi* Sowerby both correctly and for the present species. Both Frierson (1908) and Simpson (1914) seem to have partly confused *U. shuttleworthi* Lea and *Cucumerunio novaehollandiae* (Gray). Frierson speaks of *D. shuttleworthi* Lea as having a "deeply and coarsely sulcated disk" and Simpson placed it in a section *Cucumaria* (the type of which was *Unio novaehollandiae* Gray) and wrote of the shell surface as possessing "a rather strong concentric sculpture; posterior part of the shell covered with strong sub-radial, more or less nodulous ribs". He also referred to the beaks as "low, sub-compressed, sculptured with radial bars". This confusion may have been started by Lea's and Sowerby's comments on the rugose sulcations on the disk of the shell. We have examined specimens of the present species (Isaac's River, BM; Brisbane River, QM) with shell sculpturing, but nothing approaching the extensive pattern on *C. novaehollandiae*.

Types

U. shuttleworthi Lea: Holotype USNM Reg. No. 84416. Restricted type locality: South Queensland.

A. pertexta Iredale: Holotype AM Reg. No. C. 12009. Type locality: Upper Brisbane R., Qld.

A. morti Iredale: Holotype AM Reg. No. C. 61765. Type locality: Richmond R., Casino, N.S.W. Paratype AM Reg. No. C. 61766.

Description

Shell Morphology.—Shells large, up to 160 mm in length, MHI ranging from 49 to 56 per cent. Outline of juveniles elongate oval, anterior end narrower, posterior border moderately acuminate; adults range from oval to elongate oval, anterior portion of shell of varying development, BLI in the range of 22–31 per cent. Anterior margin rounded, posterior margin markedly rounded in juveniles, straight to moderately curved in adults; dorsal margin distinctly excavate anterior to the beaks, a little elevated posteriorly, more so in juveniles (BHI about 80–85 per cent.); posterior margin obliquely truncate dorsally, acuminate in young shells but rounded in adults and swamp forms, then evenly rounded ventrally. Juveniles always compressed, adults moderately to markedly swollen, especially in lagoon forms. Posterior ridge usually prominent. Beaks swollen, low, unsculptured.

Periostracum olive-brown in juveniles, brown to black in adults, often smooth and shiny, sometimes rough and heavily marked with growth lines. Nacre bluish white in juveniles, characteristically pink to reddish in shells of medium size, usually bluish or flat white in old shells, stained with pinkish or copper-coloured spots. Shell substance thick, particularly distal to the pallial line, very heavy antero-ventrally, especially in swollen forms.

Hinge variable, usually weak; cardinal teeth range from stout, erect, grooved, serrated pegs to smooth low knobs; lateral teeth long, curved, often reduced to low ridges.

Anterior muscle scars moderately to deeply impressed, retractor and adductor scars fused, retractor sometimes forming a pit beneath the cardinal tooth; posterior

scars usually weak. Beak muscle scars 3–4 in a row, usually deep. Pallial line prominent, occasionally crenate.

Anatomy.—With the characters of the genus. Siphons large but not protruding, pigmentation dark and blotchy; anal large, branchial about 1½ times size anal, bearing 2–3 rows of large papillae internally. Palps large, semilunar. Marsupium occupies middle three-fourths of inner gill of females. Outer laminae of both sexes looped, with widely spaced interlamellar junctions composed of loose connective tissue and thin unfolded epithelium. Interfilamentar junctions elongate and expanded inwards, well vascularized; water tubes narrow.

Inner gill of female similar to outer in non-marsupial region, except for slight development of muscle bundles in the interlamellar junctions. Marsupium with closely packed discontinuous interlamellar junctions consisting of dense connective tissue,

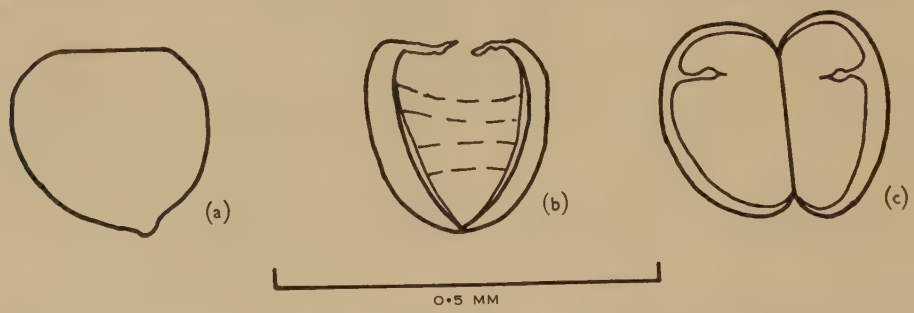

Fig. 10.—Free glochidium of *Alathyria pertexta pertexta* Iredale, Larcom Creek, Qld. (*a*) Lateral aspect; (*b*) end aspect; (*c*) ventral aspect.

large muscle bundles and thick, folded epithelium. In fully gravid marsupium, junctions largely atrophied and embryos lie loosely throughout the resulting large sac. Chitinous supporting rods usually wide, often discontinuous (Plate 18, Figs. 1 and 2).

Glochidium.—Subtriangular, swollen, measuring about 270μ in hinge plane and 250μ deep. Pronounced hooks on ventral border, to one side of centre (Fig. 10).

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. shuttleworthi Lea Holotype	106	25	24%	52	49%	42	81%	35
U. shuttleworthi Lea ex figured specimen, Sowerby 1866	125	28	22%	60	48%	48	80%	?
A. pertexta Iredale Holotype	116	30	31%	62	53%	51	82%	40
A. morti Iredale Holotype	137	27	20%	69	50%	55	80%	34
Mean 7 specimens; Calliope R., Qld. (Athearn and Clarke collections)	106	28	26%	55	52%	46	84%	32

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Mean 5 specimens; Fitzroy R. Lagoon; MCZ	129	36	27%	70	54%	61	87%	39
Mean 3 specimens; Burnett R., Gayndah; ZDQ	102	31	30%	57	56%	48	84%	33
Mean 2 specimens; Barcoo R., Blackall; ZDQ	128	34	26%	64	50%	54	84%	40
1 specimen; Flinders R., Hughenden; ZDQ	110	28	25%	62	56%	48	78%	32
Mean 5 specimens; Mackenzie R., Clermont; ZDQ	104	28	28%	55	53%	46	84%	33
Mean 12 specimens; Comet R., Comet; ZDQ	110	29	26%	61	56%	50	82%	36
Mean 12 specimens; Brisbane R., Wyvenhoe; ZDQ	116	32	28%	64	56%	54	84%	38
Mean 19 specimens; Thomson R., Aramac; ZDQ	93	25	27%	52	56%	42	81%	27

Material Examined

Types as above and specimens from QUEENSLAND: Fitzroy R. Basin, Rockhampton; Burnett R., Eidsvold, Gayndah, Mundubbera; Burdekin R., Macrossan; Yeppoon Lagoon; Dee R., near Gladstone; Calliope R., Warroo; Comet R., Comet; Kolan R., Gin Gin; Flinders R., Hughenden; Thomson R., Aramac; Mary R.; Albert R. ; Stanley R., Somerset; Brisbane R., Wyvenhoe; Lake Manchester; Barcoo R., Blackall; Dawson R.; Mackenzie R., Clermont; Boyne R. NEW SOUTH WALES: Richmond R., Casino.

Range

Coastal rivers of eastern Australia from Richmond River, New South Wales, north to Fitzroy River, Queensland, and their associated swamps and lagoons; Barcoo River (Lake Eyre drainage) and Flinders River (Gulf drainage) (Fig. 12).

ALATHYRIA PERTEXTA WARDI (Iredale)

Plate 6, Fig. 5

Quaesithyria wardi Iredale, 1943*a*, p. 191. McMichael, 1952, p. 398, photograph p. 399.

Remarks

Alathyria pertexta pertexta Iredale occurs typically in the coastal streams of northern New South Wales and north to the Fitzroy River, Queensland. Isolated occurrences are known, however, in the Barcoo River at Blackall, the Thomson River at Aramac and the Flinders River at Hughenden. These specimens, from beyond the normal range of the species, are decidedly atypical and illustrate the effect of

abnormal environment, the Blackall specimen being elongate, acuminate posteriorly and resembling *Microdontia* from New Guinea. Occurring on the north-western fringe of the range, they cannot be regarded as more than ecophenotypes of *A. p. pertexta*. In some Gulf streams of northern Queensland, however, there is a well-characterized form obviously closely related to *A. p. pertexta* yet not intergrading with it. Iredale (1943*a*) noted the similarity of this form and *Alathyria*, but on the basis of reduced and delicate hinge teeth and relatively weak muscle scars, placed it in a new genus *Quaesithyria* under the name *Q. wardi*. A second species in this genus, *Q. fleckeri* Iredale has been shown to be a synonym of *Velesunio angasi* (Sowerby). While the teeth and muscle scars of "*Q. wardi*" are weaker than in typical *A. p. pertexta*, many specimens of the latter are known, particularly large, swollen forms, with similar characters.

Museum collections contain a very limited amount of the present form, and from this an exact knowledge of its range and form cannot be obtained. Conchologically and anatomically it appears very close to and is here admitted as a subspecies of *A. pertexta*. Further collecting in north Australia may confirm this opinion or reveal it as a distinct species.

Types

Iredale did not designate a holotype for *Q. wardi*. The original description mentions two specimens, one 120 mm, the other 135 mm in length. The larger specimen was figured by McMichael (1952); the smaller is a more perfect specimen and is here selected as lectotype (AM Reg. No. C. 61767). Type locality: Einasleigh R., northern Queensland. Lectoparatypes AM Reg. No. C. 61852.

Description

Shell Morphology.—Shells large, elongate-oval, reaching about 135 mm in length, MHI about 55 per cent. Anterior portion of shell moderately developed, BLI about 25 per cent. Anterior margin rounded; ventral margin straight or slightly curved anteriorly but with an obvious sinuation near the posterior end; dorsal margin slightly excavate anterior to beaks, a little elevated posteriorly (BHI 89 per cent.), more so in young shells (BHI 83 per cent.), causing slight winging; posterior margin obliquely truncate dorsally, then sharply and squarely truncate, then rounded ventrally. Shells swollen, beaks not swollen, low, apparently smooth.

Periostracum dark brown to grey, roughened by growth lines. Nacre white, finely textured, sometimes stained bluish purple near the beaks and usually with copper-coloured or pink spots. Shell substance relatively thick, especially antero-ventrally, distal to the pallial line, frequently heavily eroded externally.

Hinge relatively weak; cardinal teeth low, smooth ridges; lateral teeth short and delicate; all teeth fairly well developed in young shells, diminished and smooth in old.

Anterior muscle scars moderately strongly impressed, adductor and retractor scars fused, protractor large, all scars often heavily roughened and pitted; posterior scars very weakly impressed. Pallial line well marked.

Anatomy.—With the characters of the genus. Siphons large but not protruding, deeply and evenly pigmented. Branchial $1\frac{1}{2}$–2 times size anal and bearing 2–3 rows

of short, stubby, pale papillae internally. Perforation in diaphragm very large. Palps very large, semilunar, and deeply ridged on opposing faces. Marsupium in female occupies four-fifths of inner gill and is anteriorly disposed. Outer gill in both sexes not obviously looped. Interlamellar junctions irregularly spaced, with fairly dense connective tissue but lacking muscle cells. Interfilamentar junctions irregular and often fused to the interlamellar junctions. All junctions bear large prominent blood vessels and a well-developed epithelium making the water tubes well defined. Inner gill of female as above in non-marsupial region. Marsupium bears few irregularly placed interlamellar junctions with folded epithelium, dense connective tissue and well-developed musculature; reduced to discontinuous finger-like septa projecting into the gill cavity. Interfilamentar junctions heavily vascularized, particularly those on the inner lamella. Chitinous rods thin and deep and generally continuous.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Lectotype	120	34	28%	64	53%	56	87%	40
Paratype	135	35	26%	75	55%	66	88%	48
Mean 3 topotypes, Einasleigh R.; AM	117	29	25%	65	56%	54	83%	43
Mean 3 juveniles, Einasleigh; AM	88	20	23%	49	56%	40	82%	30

Material Examined

As above and specimens from Lawn Hill Creek (tributary of Nicholson–Gregory system); Gregory R.; Leichardt R., SE. of Burketown.

Range

Coastal rivers of north Queensland flowing into the south-eastern corner of the Gulf of Carpentaria (Fig. 12, p. 423).

Alathyria pertexta magnifica, subsp. nov.

Plate 19, Figs. 1 and 2

Remarks

A series of shells received recently from Dutch New Guinea included four specimens of an *Alathyria*, the first of this genus to be recorded from New Guinea. The largest shell is 200 mm in length and 86 mm in maximum height, making it the largest mussel of the Australian Region with the exception of a few very elongate *Cucumerunio* specimens. In form, the shell immediately recalls *Alathyria pertexta*, but is much larger and the young stages differ in form. Geographically, the new race is close to *Alathyria pertexta wardi*, as the latter occurs in the streams flowing into the Gulf of Carpentaria, while the specimens under consideration are from streams near Merauke, Dutch New Guinea. One swamp-dwelling young shell is remarkably similar to certain phases of *Alathyria pertexta pertexta* from lagoons; the new form from New Guinea is considered to be a further subspecies of *A. pertexta*. The relationship of these shells to the specimen recorded above as *Velesunio wilsonii* (Lea) from the Maro River at Merauke remains obscure. The convergence which

is known between *V. wilsonii* and *A. pertexta* when growing under swamp conditions on the Queensland coast may be duplicated here. It is possible that the "*V. wilsonii*" from Merauke may be a very young stage of *A. pertexta magnifica*, or again, that the swamp form of *A. p. magnifica* is a large *V. wilsonii*. Only more material can solve this problem.

It should be mentioned that this large race may be related to *Unio beauforti* Bavay. As mentioned previously, under *Microdontia anodontaeformis*, we do not believe that *Unio beauforti* is related to *Microdontia*, but that it represents a species of *Alathyria*. The figure of *U. beauforti* suggests the present race in form, but is very much smaller (maximum length 70 mm). It is, of course, possible that *beauforti* is the juvenile of the present form, but with no definite knowledge of the real identity of *beauforti*, we hesitate to use that name for the present series.

The description below applies to the river shells only of *A. p. magnifica* and not to the swamp form.

Types

Holotype and two paratypes AM Reg. No. C. 62271. Type locality: Bian R., Dutch New Guinea.

Description

Shell Morphology.—Shell very large and elongate, maximum length 200 mm, MHI 43 per cent. Anterior portion of shell relatively long, BLI 25 per cent. Dorsal margin anterior to beaks long, rather straight, then curving away into the rounded anterior margin; ventral margin straight or slightly rounded, with a slight sinuation posteriorly in adult shells; dorsal margin behind beaks a little elevated, then obliquely truncate; postero-ventral margin rather blunt, posterior end of shell a little produced. Shells swollen, the beaks a little elevated and swollen, posterior ridge prominent.

Periostracum olive-brown to black, marked by fine growth lines. Nacre bluish white, stained with yellow-pink patches dorsally. Shell substance relatively thin for an *Alathyria*, not especially thickened anterior to the pallial line.

Hinge fairly strong, lamellar, consisting of very long, broad laterals, slightly serrated, double in the left valve for the posterior half of their length, single in the right; cardinals thickened, elongate, simple lamellae, a little grooved and serrated.

Anterior muscle scars firmly impressed, retractors and adductors fused; posterior scars weak; pallial line impressed and crenulate anteriorly, weak posteriorly. Beak muscle scars large, 3–5 in a row, under the beaks.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	200	50	25%	86	43%	78	91%	59
Mean 2 paratypes	143	37	26%	61	43%	52	85%	42
Maro R., swamp form; AM	125	35	28%	63	50%	50	80%	38

Material Examined

As above.

Range

Bian River, Dutch New Guinea, and (?) Upper Maro River, swamps, Dutch New Guinea.

ALATHYRIA PROFUGA (Gould)

Plate 7, Figs. 1–4

Unio profugus Gould, 1851 (in part), p. 295; 1852 (in part), p. 429; 1862, pl. 28, figs. 543, 543*a*, and 543*b*. Smith, 1881, p. 310.
Diplodon profugus (Gould) Simpson, 1914, p. 1299.
Alathyria profuga (Gould) Iredale, 1934, p. 64, pl. iii, fig. 9, pl. iv, fig. 9.
Alathyria vadena Iredale, 1943*b*, p. 90.

Remarks

Gould's description of this species was based, apparently, on two specimens, a single right valve from "Hunter's R.", the type, and a smaller shell from Parramatta. The Hunter River shell is an *Alathyria*, but the smaller Parramatta shell is *Velesunio ambiguus* (Phil.). Gould's comments on this shell must, therefore, be disregarded. Simpson (1914) remarked on this heterogeneity of the type series and doubted the validity of the species.

Gould's Hunter River shell represents a well-characterized form, common in the Hunter River drainage. It is also common in the Shoalhaven River, though the juveniles from the two localities differ, the Shoalhaven juveniles being compressed and winged. This led Iredale to name the Shoalhaven series *A. vadena*. It is considered here that these differences are not of taxonomic significance. The Shoalhaven juveniles are considered to grow rapidly and gradually assume adult form, whereas the Hunter juveniles grow slowly, develop a thicker shell and look like small adults. Perhaps further work may justify subspecific separation, but for the present *A. profuga* and *A. vadena* are synonymized.

A. profuga is in some ways atypical of *Alathyria*, but fully grown adults are closer to it than to any other genus. It is difficult to understand how Cotton and Gabriel (1932) could synonymize this large species under *Propehyridella cultelliformis* (Conrad) which name they used for *Hyridella depressa* (Lam.) and *Hyridella drapeta* (Iredale)

Types

U. profugus: Holotype USNM Reg. No. 5928, right valve only. (Original figure showed both valves.) Type locality: Hunter R., N.S.W. A paratype, also registered 5928, marked Parramatta, is *Velesunio ambiguus* Phil.

A. vadena: Holotype AM Reg. No. C. 61860. Type locality: Shoalhaven R., N.S.W. Paratypes AM Reg. No. C. 47308, C. 47310. Some juvenile paratypes, C. 12007, are from the Kangaroo R., N.S.W.

Description

Shell Morphology.—Shells medium to large, maximum length about 120 mm, MHI about 55–60 per cent. Anterior portion of shell relatively well developed, BLI 25–30 per cent. Anterior margin rounded, smoothly continuous with ventral

margin which is noticeably curved; dorsal margin curved, slightly elevated posterior to beaks then falling off gently to rounded posterior margin, not truncate.

Periostracum yellowish brown to dark brown, generally smooth, sometimes broken by marked growth lines. Nacre white, stained with copper or blue coloured spots. Shell substance moderately thick.

Hinge somewhat reduced; cardinal teeth simple thickened lamellae; lateral teeth long, reduced, sometimes disappearing in old shells. In juveniles, the teeth are well developed.

Anterior muscle scars moderately impressed, anterior adductor and retractor scars fused; posterior scars well marked. Pallial line prominent. Beak muscle scars several, deeply impressed, in a row.

Anatomy.—With the characters of the genus. Siphons large and deeply pigmented, branchial about $1\frac{1}{4}$ times size anal and bearing 2–3 rows of closely set papillae. Diaphragm relatively short and perforate. Palps large and semilunar.

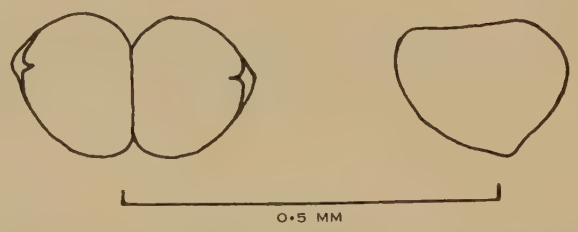

Fig. 11.—Free glochidium of *Alathyria profuga* (Gould), Williams River, Dungog, N.S.W.

Marsupium occupies at least four-fifths of inner gill of females. Outer gill of both sexes not looped and with irregularly spaced interlamellar junctions; interfilamentar junctions variable in length and strongly developed with thick epithelium packed with mucus-secreting cells and enclosing dense connective tissue containing many blood vessels. Inner gill of female as above at extremities; marsupium with closely packed, usually discontinuous interlamellar junctions consisting of thick, folded epithelium with many mucus cells, dense connective tissue and thick muscle strands. The inner ends of the septa and the inner interfilamentar junctions are densely packed with large mucus cells. Chitinous supporting rods heavy, at base of gill filaments.

Glochidium.—Subtriangular, hooked, measuring 245 μ in hinge plane, 200 μ deep (Fig. 11).

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. profugus								
Holotype	74	24	32%	41	56%	37	90%	26
A. vadena								
Holotype	120	32	24%	70	57%	58	83%	45
Hunter R., Muswellbrook; AM	38	26	29%	55	60%	47	86%	32

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Kangaroo R., Shoalhaven; AM	73	22	30%	42	58%	37	88%	22
Shoalhaven R.; AM	114	30	26%	68	60%	59	87%	40
Lake George, N.S.W.; AM	117	31	26%	69	60%	59	87%	47

Material Examined

Types as above and specimens from: Hunter R., Muswellbrook, Belltrees Station; Patterson R.; Barrington R.; Kangaroo R., Shoalhaven; Shoalhaven R.; Lake George; Williams R., Dungog.

Fig. 12.—Distribution of subfamily Velesunioninae (*continued*) and subfamily Lortiellinae. 1, *Alathyria pertexta pertexta*; 2, *A. pertexta wardi*; 3, *A. pertexta magnifica*; 4, *A. profuga*; 5, *A. condola*; 6, *Lortiella rugata*; 7, *L. froggatti*.

Range

Hunter River system and Shoalhaven River system. A specimen from Lake George was collected at least 50 years ago, before the lake dried up. Lake George has recently filled again and the occurrence of *A. profuga* will be sought with interest (Fig. 12).

Alathyria condola Iredale

Plate 7, Figs. 5–7

Alathyria condola Iredale, 1943*b*, p. 90, text fig. 1.

Remarks

This heavy, rounded, swollen species presents somewhat of a problem. Conchologically it is almost intermediate between *Alathyria* and *Velesunio*, but anatomic-

ally it resembles *Alathyria*. In many characters, it approaches *A. profuga* but is always more rounded and swollen. It apparently occurs sympatrically with *A. jacksoni*, but its shell morphology is quite different and it cannot be considered a variant of that species. Juvenile *A. condola* resemble *V. ambiguus* but have much larger and stronger teeth. Its range seems to be restricted to the Murrumbidgee and Lachlan Rivers, i.e. the north-eastern drainage to the Murray River. It is possible that *A. profuga* may have been carried over from the Shoalhaven River to this drainage, but the sum total of features characterizing the present form seems to warrant its retaining specific rank.

Types

Holotype AM Reg. No. C. 61762. Paratypes AM Reg. Nos. C. 61752, C. 61755, C. 61763. Type locality: Murrumbidgee R., Narrandera, N.S.W.

Description

Shell Morphology.—Shells large, rounded ovals of about 110 mm maximum length, MHI about 65 per cent. Anterior portion of shell moderately developed, BLI about 25 per cent. Anterior margin rounded and continuing evenly with well-rounded ventral margin; dorsal margin slightly excavate anterior to beaks, arched posterior to beaks, BHI about 82 per cent., but shell not appearing winged; posterior margin somewhat obliquely truncate dorsally then evenly rounded. Shells uniformly swollen, posterior ridge not marked; beaks low, swollen, not sculptured.

Periostracum brown in young specimens, darker in old, growth lines strong. Nacre white; shell substance thick, especially on the antero-ventral border.

Hinge strong; cardinal teeth erect, grooved lamellae in juveniles, thicker, heavy, sometimes pointed in adults; lateral teeth elongate, strong, curved.

Anterior muscle scars deeply impressed, adductor and retractor scars fused, retractor a deep pit; posterior scars moderately strong. Pallial line well marked.

Anatomy.—With the characters of the genus. Siphons large but not protruding and evenly pigmented. Branchial about twice anal and bearing 2–3 rows of large papillae internally. Palps large and semilunar. Marsupium in inner gill in female, occupying middle four-fifths. Outer gill in both sexes thin, interlamellar junctions few and widely spaced, with loose connective tissue and unfolded epithelium. Interfilamentar connections long and thin, well vascularized. Inner gill similar; marsupium has closely packed interlamellar junctions with dense connective tissue, folded epithelium, and prominent muscle strands; in fully gravid marsupium, the septa are thin and discontinuous. Chitinous supporting rods stout and rounded at base of filaments.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	91	23	26%	59	67%	47	80%	36
Mean 3 adults, Lachlan R., Condobolin; AM	101	24	24%	64	64%	56	87%	42

Dimensions (*continued*)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Mean 3 juveniles, Lachlan R., Condobolin; AM	78	19	24%	51	65%	42	82%	31
Box Ck., Cohuna; AM	84	24	28%	55	63%	45	82%	36

Material Examined

Types and from Lachlan R., Condobolin; Box Ck., Cohuna; Murrumbidgee R., Darlington Point, Narrandera, Yanco.

Range

Apparently confined to north-eastern streams of the Murray River drainage (Fig. 12).

Genus WESTRALUNIO Iredale

Westralunio Iredale, 1934, p. 62. Type species by original designation: *Westralunio ambiguus carteri* Iredale, 1934 (= *Westralunio carteri* Iredale).

Remarks

The genus was erected for one species of velesunionine mussel, restricted to the south-western corner of Australia, the species being separable by its very strong, serrated cardinal teeth. Modell (personal communication) suggested that the New Guinea species, *Unio flyensis* Tapparone Canefri, belonged in this genus and this arrangement was followed by McMichael (1956). Subsequently a new form of *Westralunio* has been described from New Guinea (*W. albertisi* Clench) so that the definition of the genus is here broadened to include the New Guinea forms. The seemingly anomalous distribution of the species of this genus suggests, perhaps, morphological convergence, but it is also possible that these species are the remnants of a once widely distributed genus.

Description

Shell Morphology.—Freshwater mussels of the subfamily Velesunioninae of small size, not exceeding 70 mm in length. Shells oblong-ovate to rounded, hinge-line curved, hinge strong unionid, consisting of typical laterals and erect, serrated, thick cardinals. Beaks always smooth, shell substance typically thick. Shells of medium width, posterior ridge rather pronounced. Anterior muscle scars strongly impressed. Periostracum smooth, dark brown, with fine growth lines.

Anatomy.—No supra-anal opening. Siphons of moderate size, not prominent, pigmented dark brown; branchial siphon about $1\frac{1}{2}$ times size of anal and bearing papillae internally; gill diaphragm relatively long and perforate. Outer lamellae of outer gills completely fused to mantle, inner lamellae of inner gills fused to visceral mass then united to form diaphragm. Palps relatively small, subtriangular to semi-lunar in shape. Marsupium well developed as a very distinct swollen pouch in the middle third of the inner gill of females. Outer gill in both sexes thin, with numerous, short interfilamentar junctions and few, irregular interlamellar junctions. Inner gill in females similar, but marsupium possesses numerous, closely packed, well-developed interlamellar junctions (Plate 17, Figs. 4 and 5).

Glochidium.—Unknown.

Distribution

South-western Australia and southern New Guinea.

Differential Diagnosis of Species

W. carteri Iredale and *W. flyensis* (Tapparone Canefri) are rather similar in shell morphology, being oblong-ovate species. *W. carteri* reaches a larger size and is slightly more winged; it is squarely truncate posteriorly, whereas *W. flyensis* is obliquely truncate. *W. albertisi* Clench is a high, rounded species, almost circular in outline.

Relationships

Westralunio is, in most respects, a typical velesunionine mussel, but it is easily distinguished from the related genera, *Velesunio* and *Alathyria*, by its strong, grooved cardinal teeth.

Westralunio carteri Iredale

Plate 8, Figs. 1–10; Plate 17, Figs. 4 and 5

Unio australis Lamarck, Menke, 1843, p. 38, specimen 219. (Non *Unio australis* Lam. 1819.)
Unio moretonicus Reeve, Smith, 1874, p. 3, pl. iv, fig. 2. (Non *U. moretonicus* Reeve 1865.)
Hyridella australis (Lam.), Cotton and Gabriel, 1932 (in part), p. 156. (Non *U. australis* Lam. 1819.)
Hyridella ambigua (Philippi), Cotton and Gabriel, 1932 (in part), p. 157. (Non *U. ambiguus* Phil. 1847.)
Westralunio ambiguus carteri Iredale, 1934, p. 62.
Westralunio ambiguus (Philippi), Iredale, 1934, p. 62, pl. iii, fig. 8, pl. iv, fig. 8. (Non *U. ambiguus* Phil. 1847.)
Centralhyria angasi subjecta Iredale, 1934, p. 67 (in part).

Remarks

Despite the distinctiveness of this species, it was not recognized as such until 1934, by Iredale. Menke (1843) first recorded mussels from south-western Australia, collected in 1836 and 1842 by Preiss, under the name *Unio australis* Lam., but the Western Australian mussels are very different from that species. The shell figured by Smith (1874) has an interesting history. Iredale (1934, p. 70) has shown that the shells figured on Smith's plate iv were "Beagle" specimens, not "Erebus" and "Terror". He determined the figured "*Unio moretonicus* Reeve" as a Northern Territory shell and named it *Centralhyria angasi subjecta*, and assumed that "Membridge River", listed by Smith as the locality, was somewhere in northern Australia, the area from which the other "Beagle" shells on plate iv were collected. Dr. W. J. Rees has kindly supplied photographs of two specimens in the British Museum. One, Reg. No. 40-10-21-29, is without doubt the specimen figured by Smith. This shell is not from the Membridge River, but from the Avon River, Western Australia, presented by Mrs. J. Gould, and is a large *Westralunio carteri*. The other specimen, at first thought to be Smith's figured specimen, differs slightly in form and corrosion characters. A pencilled locality inside the shell looks like "Membridge R." but closer scrutiny has shown this not to be so. The word could be a scribbled form of "Murrumbidgee" and indeed the shell closely resembles

Velesunio ambiguus known from that stream. The shell bears the registered number 1844-12-8-15 but Dr. Rees states that that number does not occur in the Register. The specimen has been re-registered 1952-10-28-1. It is figured here, Plate 8, Figures 8–10.

It appears that when the plate of "Beagle" shells was prepared, the Avon River specimen was inadvertently figured. The plate was mislaid for 30 years until Smith in 1874 assumed that it was associated with the "Erebus" and "Terror" report, published it and mistook the "Membridge R." specimen for the figured one. Since the shell figured is *W. carteri* and since Iredale's (1934) *Centralhyria angasi subjecta* was based, in part, on this figure, it must be considered a partial synonym. Iredale did not designate a type for his subspecies nor can a specimen labelled with this name be found in the Australian Museum. The figured Avon River specimen is here selected as lectotype so that the name will fall in the synonymy of *W. carteri*.

The exact origin of the "Membridge R." shell is uncertain. If it was from the Murrumbidgee River, as is quite possible, it is unlikely to have been a "Beagle" shell, the "Beagle" zoologists not having visited that area. It does not resemble any northern or north-western Australian shell, nor is there a river in that region whose name remotely resembles "Membridge".

Iredale (1934), recognizing the distinctiveness of the Western Australian mussel, created the genus *Westralunio* for it and used the name *ambiguus* Philippi, although that name had long been associated with eastern Australian shells. His allocation of this name was based on the resemblance of south-western Australian mussels to Philippi's figure and because the latter shell came from Parreyss who had obtained other material from Preiss who collected in this region. In case of error, Iredale made a new subspecies, *Westralunio ambiguus carteri*, type of the genus, in order that the generic name would be associated with the Western Australian mussel and not the name *ambiguus* Philippi.

Our remarks on *Velesunio ambiguus* (Phil.) above make it clear why the name *ambiguus* Phil. cannot be applied to Western Australian mussels. Iredale recognized two subspecies in *Westralunio*, the typical *ambiguus ambiguus* from King George's Sound and surrounding streams and *ambiguus carteri*, a more elongate, larger form from Victoria Reservoir, near Perth. Examination of a large series of shells from many localities in south-western Australia indicates that Iredale's distinction cannot be valid. Separation is not possible on anatomical or geographical grounds. In view of the above findings, the name *Westralunio carteri* Iredale 1934 will apply to this species.

Types

Iredale did not designate a holotype for *Westralunio ambiguus carteri*. The syntypes are in the AM, Reg. No. C. 61724. The specimen figured here (Plate 8, Figs. 1–4) is selected as lectotype. Type locality: Victoria Reservoir, Darling Range, 12 miles east of Perth, W.A.

The lectotype of *Centralhyria angasi subjecta* Iredale, here selected, is BM Reg. No. 1840-10-21-29. Type locality: Avon R., W.A.

Description

Shell Morphology.—Shells oblong-ovate, small to medium-sized, maximum length not exceeding 70 mm, MHI 60–70 per cent. Anterior portion of shell moderately

developed, BLI 26–29 per cent. Anterior margin evenly rounded; ventral margin slightly curved, but straighter in larger shells, continuing smoothly into posterior margin but a postero-ventral deflection is prominent in larger shells; dorsal margin curved, slightly elevated behind beaks, but not producing marked winging, then rather squarely truncated posteriorly. Shells not swollen; beaks not swollen; usually corroded, always smooth.

Periostracum dark-brown to black often with a reddish ferruginous deposit; growth lines fine and regular. Nacre dirty white, stained purple or brown beneath the beaks, often with copper-coloured blotches.

Hinge strong, hinge-line curved. Two cardinal teeth in right valve, both flattened, grooved, and serrated in young shells, the upper remaining flat but reduced in older shells, the lower thickening but retaining serrations; single left cardinal triangular, erect, grooved, and serrated in young shells, becoming thicker and smoother in old. Right lateral flat, erect, sometimes grooved along its edge; left lateral double, the lower tooth the larger, both flat, erect, and grooved internally. All teeth show a gold metallic lustre in most living, young specimens.

Anterior muscle scars deeply impressed, anterior retractor scar forming a pit under the cardinal tooth but continuous with adductor scar. Posterior muscle scars lightly impressed. Beak muscle scars 2 or 3, deeply impressed, irregularly situated. Pallial line not prominent.

Anatomy.—No supra-anal opening; siphons of moderate size, pigmented, branchial about 1½ times size anal and with 2–4 rows of papillae internally; siphons separated by mantle bridge continuous with gill diaphragm which is perforate. Palps very small, subtriangular, and free except on dorsal border. Outer lamellae of outer gills completely fused to mantle; inner lamellae of inner gills fused to visceral mass, then united for half their length to form a diaphragm. Marsupium well developed, occupying middle half of inner gill in females. Outer gill in both sexes thin, with numerous short interfilamentar junctions and few, irregular interlamellar junctions, all with well-developed walls; blood spaces numerous and large. Inner gill in females as above in non-marsupial portion; marsupium with numerous closely packed interlamellar junctions possessing thick, moderately folded walls and moderate muscle development. Inner gill grooved at base. Chitinous supporting rods large, at base of gill filaments (Plate 17, Figs. 4 and 5).

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
W. carteri								
Lectotype	43	11	26%	30	70%	26	87%	18
Mean 5 specimens; Blackwood R.; AM	61	16	26%	37	61%	33	89%	23
Mean 32 specimens; Serpentine R.; ZDQ	49	14	29%	31	63%	26	86%	18
C. angasi subjecta								
Lectotype	57	16	28%	34	60%	31	91%	?

Material Examined

Type specimens as above and from: Serpentine R.; Blackwood R., Busselton; Preston R.; Main Drain, Peel Estate; Claremont Swamps, near Perth; Bow R.; Avon R.; Victoria Reservoir, Darling Ranges; Canning R.; Wongong R.; Vasse R.; Collie R.; Warren R.; Frankland R.; King George's Sound.

Range

South-western corner of Western Australia, west of King George's Sound and north to Avon River (Fig. 8).

WESTRALUNIO FLYENSIS (Tapparone Canefri)

Plate 8, Figs. 11–14

Unio (*Bariosta*) *flyensis* Tapparone Canefri, 1883, pp. 293–4, text fig. 1.
Diplodon (*Hyridella*) *flyensis* (Tapp. Can.), Simpson, 1914, p. 1295.
Hyridella flyensis (Tapp. Can.), Haas, 1924, pp. 74–5, pl. ii, figs. 4 and (?)5.
Westralunio flyensis (Tapp. Can.), McMichael, 1956, p. 41.

Remarks

This species, though known until recently (McMichael 1956) only from the Fly River, Papua, and doubtfully from Sabang Village, Dutch New Guinea, is quite distinctive and is closely related to *W. carteri* Iredale from Western Australia. Its range is now known to extend over most of the southern rivers of New Guinea; throughout its range it maintains constancy in form. Its relationship to Australian forms was first suggested by Simpson (1914) when he assigned it to the Australian group *Diplodon* (*Hyridella*).

Types

According to Haas (1924) the holotype is in the Museo Civico di Storia Naturale, Genoa, Italy. Type locality: Fly R., Papua. Haas (loc. cit.) has figured this specimen (pl. ii, fig. 4).

Description

Shell Morphology.—Shells oblong-ovate, small, maximum length about 60 mm, MHI 65–70 per cent. Anterior portion of shell moderately short, BLI 15–25 per cent. Anterior margin evenly rounded, ventral margin slightly curved, dorsal margin evenly curved, slightly elevated posteriorly then obliquely truncate, posterior margin forming a slight ventral deflection. Shells not swollen, posterior ridge not prominent, beaks apparently smooth.

Periostracum olivaceous brown to reddish brown with fine growth lines. Nacre whitish, iridescent towards posterior margin. Shell substance relatively thick.

Hinge strong; cardinal teeth small, compressed, serrated and grooved, and apparently double in each valve; lateral teeth short and curved.

Anterior muscle scars deeply impressed, retractor and adductor scars fused; posterior scars lightly impressed; beak muscles scars few. Pallial line moderately impressed.

Anatomy.—With the characters of the genus. Siphons not prominent, branchial about $1\frac{1}{4}$ times anal and bearing 1–2 rows of very small papillae, internally.

Diaphragm relatively long, perforate. Palps relatively large, semilunar. Marsupium a small but very distinct pouch anteriorly in the inner gill of females. Outer gill in both sexes looped, with regular interlamellar junctions; interfilamentar junctions long, thin-walled; blood vessels few. Inner gill of female as above in non-marsupial region. Marsupium very distinct, swollen, with well-developed interlamellar junctions, mostly discontinuous, with moderately folded walls, fairly thin epithelium, diffuse connective tissue, and prominent muscle strands. Chitinous supporting rods variable.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype, ex Tapp. Can., 1883, and Haas, 1924	49	12	25%	35	68%	29	83%	19
1 specimen, Fly R.; AM	59	9	15%	39	66%	30	77%	20
1 specimen, Strickland R.; AM	32	6	18%	22	68%	17	77%	12
Mean of 5 specimens, St. Joseph's R., Aipiana; QM	40	10	25%	25	63%	22	88%	14

Material Examined

Specimens from Fly R., Papua; Strickland R., Papua; Kikori R., Middletown, Papua; St. Joseph's R., Aipiana, Papua; Kali Maak, tributary of Digoel R., near Tanah Merah, D.N.G.

Range

Southern rivers of New Guinea (Fig. 8).

Westralunio albertisi Clench

Plate 8, Figs. 15 and 16

Westralunio albertisi Clench, 1957, pp. 3–4, text fig. 2.

Remarks

This recently described form differs sufficiently from *Westralunio flyensis* in shell morphology to be provisionally ranked as a full species. It is possibly a very well-defined ecotype, the product of the lake environments in which it seems to occur; however, as we do not consider polytopic subspecies to be worthy of taxonomic recognition, we do not rank it as such, but prefer to leave it as a full species until such time as its true nature can be determined. In range it is macrogeographically sympatric with *W. flyensis* but the only two localities from which it is recorded are probably lake or swamp type habitats, while *W. flyensis* is known only from rivers.

Types

Holotype MCZ Reg. No. 212908. Paratype AM Reg. No. C. 62268. Type locality: inland from Daru, Papua. An additional paratype from Lake Murray, Papua, is in the MCZ.

Description

Shell Morphology.—Shells subcircular, small, maximum length about 60 mm, MHI 79–88 per cent. Anterior portion of shell moderately short, BLI 21–24 per cent. Anterior margin short and straight then sharply and obliquely truncate, becoming evenly rounded below and continuing into the rounded ventral margin; dorsal margin slightly curved and elevated, then sharply and obliquely truncate, the shell appearing noticeably winged; posterior margin meeting the rounded ventral margin in a blunt angle. Shells comparatively swollen, the posterior ridge marked, the posterior slope compressed, beaks low, apparently smooth.

Periostracum dark brown with fine growth lines. Nacre bluish white, iridescent. Shell substance relatively thick. Hinge strong; cardinal teeth moderately large, erect and grooved; lateral teeth elongate, strong, curved, double in the left valve, single in the right.

Anterior muscle scars deeply impressed, retractor and adductor scars fused; posterior scars lightly impressed; beak muscle scars 2, the posterior quite deeply impressed.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype, ex Clench (1957)	53	12	23%	42	79%	35	83%	20
Paratype; AM	51	11	21%	45	88%	35	78%	22
Paratype, Lake Murray; ex Clench (1957)	57	?	?	50	88%	?	?	25

Material Examined

Paratype from inland from Daru, Papua.

Range

Lakes (?) of the Fly River district, Papua.

Subfamily **LORTIELLINAE** Iredale

Subfam. Lortiellinae Iredale, 1934, pp. 58 and 77.

Remarks

The subfamily Lortiellinae was erected for one genus, *Lortiella*, which differed considerably in shell morphology from other Australasian mussels. The first species described in this group, *L. rugatus* (Sowerby), was originally placed in the South American genus *Mycetopus*, being of typical mycetopodine facies. The mycetopodine forms of south-east Asia were separated by Conrad (1868) to a new genus *Solenaia* into which Simpson (1900, 1914) placed *L. rugatus*.

Iredale (1934) commented that "The shell (of *L. rugatus*) does not look much like a *Solenaia*, and seems to be an elongate relation of the *angasi* or *stuarti* series (= *Velesunio* spp.), but obviously distinct from either". He separated the two

Australian species to a new genus *Lortiella*. In his introductory remarks, he gave "beaks ridged" as the only diagnosis for the subfamily, but all the specimens examined in the present work have smooth beaks; the subfamily must, therefore, be redefined.

Modell (1942) accepted both the genus and the subfamily, but included *Solenaia* Conrad as well. While *Lortiella* and *Solenaia* are possibly related, they are certainly generically distinct. Unfortunately, no whole specimens of *Lortiella* have been available in the present work and the anatomy of the genus remains unknown. The anatomy of *Solenaia soleniformis* (Benson) (= *S. bensoni* Lea) has been described by Prashad (1919). While this account may not typify the genus, several key anatomical features are revealed. These are the presence of a supra-anal opening, marsupium in all four gills and elongate labial palps. These features contrast strongly with those of any Australasian mussel so far examined, and it is obvious that the correct relationship of *Lortiella* will be established only when its anatomy is known.

Under the present circumstances, since *Lortiella* does not fit conveniently into any other subfamily of Australasian mussels, Iredale's subfamily for the genus is here accepted, with the necessary redescription.

Diagnosis (shell morphology only)

Freshwater mussels of the family Mutelidae (?), of mycetopodine facies, very elongate, tapering anteriorly. Beaks smooth; hinge primitively lamellar, reduced, sometimes almost absent. Shell surface smooth.

Present Distribution

North-western Australia.

Fossil Record

If Modell's (1949) concept of the subfamily is accepted, his (1942) record of fossils of the group from the Pliocene in China is pertinent. No fossils are known from the Australian region.

Genus LORTIELLA Iredale

Lortiella Iredale, 1934, p. 70. Type species by original designation: *Mycetopus rugatus* Sowerby, 1868*c*.

Remarks

This genus was never adequately described by Iredale, nor was the type species designated in a formal manner. However, Iredale's comment, under the heading of *Mycetopus rugatus*, "To relieve it of its present very anomalous position, the new generic name *Lortiella* is introduced", leaves no doubt that *M. rugatus* is the type species. Iredale's description of a second species, *L. froggatti*, gave clear indication of generic characters. Unfortunately no anatomical details are available for either species; these, when found, will throw light on the exact relationship of the genus to other Australasian genera.

Diagnosis

Shell Morphology.—Freshwater mussels of the subfamily Lortiellinae Iredale, of mycetopodine facies, reaching about 100 mm in length, MHI 35–40 per cent.

Outline somewhat adze-shaped, tapering anteriorly, somewhat winged posteriorly. Hinge simple, with elongate lamellar teeth in juveniles, sometimes almost disappeared in adults. Beaks slightly elevated, unsculptured. Muscle scars lightly impressed.

Anatomy.—Unknown.

Glochidium.—Unknown.

Distribution

North-western Australia.

Differential Diagnosis of Species

The two species can be recognized thus: *L. rugata* (Sowerby) has a very reduced hinge and is squarely truncate posteriorly, while *L. froggatti* Iredale has a stronger hinge and is obliquely truncate and rounded posteriorly.

Relationships

The genus can be distinguished from all other Australian groups by its relatively low MHI and lack of beak and shell sculpture. In general shape it approaches *Velesunio wilsonii* which has a constantly higher MHI, and the south-east Asian genus *Solenaia* which is larger, with thicker shell, and is geographically distant. The main affinities of the genus appear to lie with *Solenaia* but, as discussed above, the question remains an open one. There are no fossils of the genus known.

Lortiella rugata (Sowerby)

Plate 9, Figs. 1 and 2

Mycetopus rugatus Sowerby, 1868*c*, pl. iii, sp. and fig. 7. Clessin, 1875, p. 205, pl. 67, fig. 4. Smith, 1874, p. 3, pl. iv, fig. 1; 1881, p. 313.

Solenaia rugatus (Sowerby), Simpson, 1900, p. 657; 1914, p. 462.

Lortiella rugata (Sowerby), Iredale, 1934, pp. 70–1; 1943*a*, p. 190.

Note: Martens, in Zoological Record for 1868, p. 503, mistakenly recorded Sowerby's species as *Mycetopus plicatus* (this species appears on the previous page of Conchologica Iconica).

Remarks

This species was first collected from the Victoria River, Northern Territory, during the second voyage of the "Beagle". Iredale (1934) has revealed that the specimens figured on plate iv in Smith's (1874) report were not from the voyage of the "Erebus" and the "Terror" as indicated by Smith, but from the second voyage of the "Beagle"; the plate was prepared for Stokes's (1846) book but was never published in it. The "Beagle" shells were eventually deposited in the British Museum and were later described by Sowerby.

Types

The type series of *L. rugata* is in the BM, consisting of specimens numbered 41-11-25-59 to 41-11-25-67. None of these specimens fits Sowerby's (1868*b*) figure, but this appears to be somewhat inaccurate and may have been a composite sketch. A photograph of more material, numbered 44-1-12-160, has been kindly supplied by Dr. W. J. Rees; it shows two valves which are not a pair. The smaller valve is the one figured by Smith (1874) and since this figure was prepared for Stokes's (1846) report, the specimen is obviously from the type series. Since the specimen figured by Sowerby is unidentifiable and Sowerby did not designate a type, Smith's specimen is here selected as lectotype. Type locality: Victoria R., Northern Territory.

Description

Shell Morphology.—Shells very elongate, MHI about 35 per cent.; anterior end relatively short, BLI about 25 per cent. Anterior margin rounded, ventral margin straight or slightly sinuate in the middle; dorsal margin posterior to the beaks long, straight, and somewhat elevated, BHI about 75 per cent., giving the shell a gradual taper towards the anterior end; posterior margin almost squarely truncate, meeting the ventral margin in a rounded angle. Shells slightly swollen, a little compressed anteriorly, posterior ridge not marked, beaks slightly swollen, low and without sculpture.

Periostracum dark, olive-brown with noticeable concentric growth lines; nacre dull white, stained anteriorly. Shell substance relatively thick and strong.

Hinge reduced, cardinal and lateral teeth discernible only as ridges in adult shells.

Anterior muscle scars lightly impressed, retractor and adductor fused. Posterior scars and pallial line very light.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Lectotype	81	18	22%	27	33%	20	70%	?
Mean 6 paratypes	92	24	26%	32	35%	25	78%	?
Katherine R., Mambulloo; SAM								
Adult	64	14	22%	23	36%	17	74%	18
Juvenile	32	8	25%	13	40%	9	69%	9

Material Examined

Shells only, from Katharine and Victoria Rivers, Northern Territory.

Range

Known only from the above rivers (Fig. 12).

Lortiella froggatti Iredale

Plate 9, Figs. 3–5

Lortiella froggatti Iredale, 1934, p. 71, pl. v, fig. 5, pl. vi, fig. 5; 1943*a*, p. 190. McMichael, 1952, p. 397, fig. on p. 398.

Remarks

Little can be added to Iredale's original description of the present species, no further material having been collected, except one shell in 1953 from the Fitzroy River, by N. B. Tindale, which agrees in all respects with the type series. Compared with *L. rugata* (Sowerby) the species is quite different in appearance, but the localities for the two species are some hundreds of miles apart and it must be emphasized that the vicissitudes of the environment in most north Australian streams are such that ecophenotypical differences can be considerable. It is possible, therefore, that

later collecting, permitting anatomical examination and providing additional shell material, may show the two to be conspecific. On the material available, we accept Iredale's separation of the species.

Types

Holotype AM Reg. No. C. 61862. Paratypes AM Reg. No. C. 61863. Type locality: Lennard R., north Western Australia.

Description

Shell Morphology.—Shells elongate, maximum length about 60 mm, MHI about 40 per cent. Anterior end relatively long, BLI about 30 per cent. Anterior margin rounded; ventral margin straight or slightly curved; dorsal margin posterior to beaks somewhat elevated and straight, BHI about 80 per cent., then obliquely truncate; posterior margin rounded. Shells swollen posteriorly, compressed anteriorly, posterior ridge rounded; beaks swollen and elevated, apparently smooth.

Periostracum yellow-brown, marked by fine growth lines. Nacre bluish, iridescent. Shell substance thin.

Hinge weak, lamellar; one cardinal tooth in each valve; one elongate lateral in right valve, two weaker laterals in left.

Anterior muscle scars very lightly impressed, retractor and adductor fused; posterior scars and pallial line almost invisible.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	58	16	28%	25	43%	19	76%	16
Mean 7 paratypes	49	14	29%	20	41%	17	85%	14

Material Examined

Shells only from Lennard R. and Fitzroy R., Myroodah Crossing, north Western Australia.

Range

Known only from the above rivers (Fig. 12).

Subfamily **HYRIDELLINAE** Iredale

Subfamily Propehyridellinae (= Hyridellinae) Iredale 1934, p. 58.

Remarks

The subfamily Propehyridellinae Iredale, based on the genus *Propehyridella* Cotton & Gabriel, had best be changed to Hyridellinae in conformity with Article 5 of the old International Rules of Nomenclature since it has been shown (McMichael 1955) that *Propehyridella* is a junior objective synonym of *Hyridella* Swainson. Although the Copenhagen Decisions would make this change unnecessary, it is felt that the well-known name *Hyridella* is more suitable as the basis for the familial name, especially as the Copenhagen Decisions are, at the time of writing, not yet in force and Hyridellinae has already been used on several occasions.

Iredale's diagnosis of the subfamily stated simply "Beaks plicate [= sculptured]. Shell small". At that time, it served to differentiate the subfamily from the only other Australian group with sculptured beaks, the Cucumerunioninae, represented in Australia by only one species of very large size. The expansion of the latter group to include a number of species of small size demands redefinition of both groups.

Three genera were included originally in the subfamily, viz. *Propehyridella* Cotton & Gabriel, *Protohyridella* Cotton & Gabriel, and *Rugoshyria* Iredale. Iredale (1943*b*) subsequently transferred the genus *Hyridunio* Iredale to the group, since it proved to have sculptured beaks. In the present account the genera *Rugoshyria* and *Hyridunio* are placed in the synonymy of the genus *Hyridella* (= *Propehyridella*) while *Protohyridella* is admitted as a subgenus only of *Hyridella*.

Iredale's original treatment dealt only with Australian species, but the group includes, as well, most New Zealand mussels and two Melanesian species. The latter were placed by Haas (1924) in the genus *Virgus* Simpson, but separated subgenerically under *Leiovirgus* Haas. *Virgus*, s.s., is considered here to belong to the subfamily Cucumerunioninae, but the species included in *Leiovirgus* agree anatomically and conchologically with *Hyridella* Swainson. One of the species, *Unio guppyi* Smith, is, however, regarded as subgenerically separable from *Hyridella*.

Two New Zealand species are referable to *Hyridella* but one of these requires subgeneric separation.

The subfamily Hyridellinae contains, therefore, only the one genus *Hyridella*.

Diagnosis

Freshwater mussels of the family Mutelidae typically of unionine facies with relatively solid, elongate shells, beaks sculptured with V-shaped ridges and, in some, shell sculpture variously developed. Hinge typically unionid, cardinal teeth generally erect and grooved; anterior retractor muscle scar tending to separate from the adductor scar as a deep pit beneath the cardinal teeth, anterior scars usually deeply impressed. Siphons well developed and prominent, gill diaphragm medium to long, usually perforate, palps small and subtriangular. Marsupium well developed in middle third of inner gill of females. Glochidium subtriangular, hooked.

Present Distribution

Eastern Australia, Tamar River system of Tasmania, North and South Islands of New Zealand; Solomon Islands and New Guinea.

Fossil Record

Represented in Australia by some Mesozoic forms, possibly Triassic; known doubtfully from the Pliocene of New Zealand; not known from Melanesia.

Genus HYRIDELLA Swainson

Hyridella Swainson, 1840, pp. 285 and 380. Type species by monotypy: *Unio australis* Lamarck, 1819.

Leiovirgus Haas, 1912, p. 132. Type species by original designation: *Unio misoolensis* Schepman, 1897.

Nesonaia Haas, 1912, p. 137. Type species by original designation: *Unio guppyi* Smith, 1885.

Propehyridella Cotton & Gabriel, 1932, p. 158. Type species by original designation: *Unio nepeanensis* Conrad, 1850.

Protohyridella Cotton & Gabriel, 1932, p. 159. Type species by original designation: *Unio glenelgensis* Dennant, 1898.

Hyridunio Iredale, 1934, p. 68. Type species by original designation: *Hyridunio australis drapeta* Iredale, 1934.

Rugoshyria Iredale, 1934, p. 71. Type species by original designation: "*Unio paramattensis* Lea, 1862 = *Unio depressa* Lamarck, 1819".

Remarks

McMichael (1955) has discussed both the validity of the genus *Hyridella* Swainson and the identity of its type species, *Unio australis* Lamarck. He has also set out arguments for the retention of the name *Hyridella* and its continued association with *U. australis*. The name *Hyridella* has been variously applied. Simpson (1900, 1914) used it as a subgenus of *Diplodon* Spix for nearly all of the Australian and New Zealand mussels, including "*australis* Lamarck", which name he used for *Velesunio ambiguus* (Phil.). Suter (1905, 1913) followed Simpson's use of *Hyridella* for New Zealand mussels. Ortmann (1912), following Simpson, misidentified *V. ambiguus* as "*australis*" and used the name *Hyridella* generically for it. Haas (1924) followed Ortmann's use of the name, i.e. for velesunionine mussels, and applied it to several New Guinea species; he placed other New Guinea species in *Leiovirgus* Haas which he ranked as a subgenus of *Virgus* Simpson. Cotton and Gabriel (1932) still followed Simpson and Ortmann in using *Hyridella* for velesunionine mussels, but recognized that several Australian species differed from them and erected two genera to accommodate them. The genera were *Propehyridella* with *Unio nepeanensis* Conrad as type and *Protohyridella* with *Unio glenelgensis* Dennant as type.

Iredale (1934) did not accept the usual identification of *Unio australis* Lam., rejected the name *Hyridella* as not applying to any Australian species and proposed a new name, *Hyridunio*, for the form he had identified as *australis*. He designated a subspecies, *Hyridunio australis drapeta*, as type so that, in case he had misidentified *australis*, the name *drapeta* rather than *australis* should be associated with *Hyridunio*. More recently Dell (1953) has used, with reservation, the name *Hyridella* for the two species of mussels he recognizes in New Zealand.

Now that the identity of *Unio australis* Lam. has been determined and the name *Hyridella* Swainson preserved in association with that species, a detailed consideration of the genus *Hyridella* has become necessary. In the present work, a large series of mussel species, all possessing sculptured beaks, has been examined. Two quite clear-cut groups can be recognized, one typically without shell sculpture and with erect cardinal teeth, the other typically with shell sculpture and heavy, grooved, serrated cardinals. The first group is placed in the subfamily Hyridellinae Iredale, the other in the subfamily Cucumerunioninae Iredale.

Within the subfamily Hyridellinae, there are several generic names based on different nominal species which should be considered here. These are *Hyridella* Swainson, *Leiovirgus* Haas, *Nesonaia* Haas, *Propehyridella* Cotton & Gabriel,

Protohyridella Cotton & Gabriel, *Hyridunio* Iredale, and *Rugoshyria* Iredale. For the following reasons, these are all placed in the synonymy of *Hyridella* Swainson.

(1) *Leiovirgus* Haas has been ranked previously as a full genus, separable from *Hyridella* on beak sculpture characteristics. However, its type species (*Unio misoolensis* Schepman) as detailed below, proves to have typical *Hyridella* sculpture, so *Leiovirgus* is now placed as a junior subjective synonym of *Hyridella* s.s.

(2) *Nesonaia* Haas has for some time been considered a synonym of *Leiovirgus* Haas. However, its type species, *Unio guppyi* Smith, does differ from *Hyridella* species in beak sculpture, though not sufficiently for generic distinction. It is, however, worthy of subgeneric separation.

(3) The type of *Propehyridella* (*U. nepeanensis* Conrad) is a junior synonym of *U. australis* Lamarck, and *Propehyridella* becomes, therefore, a synonym of *Hyridella* s.s.

(4) The type species of *Protohyridella* (*U. glenelgensis* Dennant) possesses distinctive shell sculpture, but is close to *Hyridella* in all other characters. It cannot be separated generically, but is worthy of subgeneric distinction.

(5) Iredale was in error in identifying *U. australis* Lamarck, but since he designated a subspecies, *H. australis drapeta* Iredale, as type of *Hyridunio*, his concept of *Hyridunio* is quite clear. *H. drapeta* is a characteristic form, obviously and closely related to *H. australis*. *Hyridunio* therefore becomes a junior subjective synonym of *Hyridella* s.s.

(6) *Rugoshyria* Iredale, erected for *Unio depressa* Lam. and related species, cannot be separated taxonomically from *Hyridella* s.s. and is therefore placed in synonymy with it.

The genus *Hyridella*, as regarded and defined in the present work is a fairly homogeneous unit. Within the genus four "species groups" are distinguishable and these groups are placed subgenerically as follows:

(1) *Hyridella*, s.s., including *H. australis* (Lam.), *H. depressa* (Lam.), *H. drapeta* (Iredale), *H. narracanensis* (Cotton & Gabriel), *H. aucklandica* (Gray), and *H. misoolensis* (Schepman).

(2) *Nesonaia* Haas, including *H. guppyi* (Smith).

(3) *Protohyridella* Cotton & Gabriel, including *H. glenelgensis* (Dennant).

(4) A new subgenus, *Echyridella*, erected for the New Zealand species *H. menziesi* (Gray).

Diagnosis

Shell Characters.—Freshwater mussels of the subfamily Hyridellinae of small to medium size reaching about 100 mm in length. Shells variable in form tending to be elongate, MHI 45–60 per cent.; typically of unionine facies; hinge-line usually gently curved, hinge usually strong unionid, sometimes reduced; cardinal teeth usually erect, grooved, sometimes reduced; beaks sculptured with V-shaped ridges, tending to separate below, but sometimes extending to surface of shell; shells typically not swollen; shell substance of variable thickness; anterior muscle scars

firmly impressed, retractor and adductor usually separate, but even where fused retractor tends to occur as a deep pit under the cardinal teeth.

Anatomy.—Supra-anal opening absent; siphons prominent, protruding and of medium size; mantle bridge well developed, siphonal area usually deeply pigmented; branchial siphon about $1\frac{1}{2}$ times size anal, open below and bearing a variable number rows of relatively large papillae; gill diaphragm of medium length; outer gill triangular, attached completely to mantle by outer lamella and to inner gill by inner lamella; inner gill elongate, attached posteriorly to gill diaphragm, dorsally and anteriorly to foot by inner lamella; gill diaphragm perforate or imperforate; palps of medium size, typically triangular, outer palp fused to mantle on dorsal half. Marsupium occupies middle third of inner gill of female; interlamellar junctions of marsupium closely packed, of variable structure, usually with a spacious sinus at one or both ends (Plate 18, Figs. 3–5).

Glochidium.—Subtriangular, hooked, of varying size. Breeding apparently seasonal, from spring through summer.

Distribution

Eastern Australia, south of the Tropic of Capricorn; Tamar River system of Tasmania; North and South Islands of New Zealand; Solomon Islands; Island of Misool (Dutch New Guinea) and south coast rivers of New Guinea.

Differential Diagnosis of Subgenera

The four subgenera included in this genus can be distinguished as follows: *Hyridella*, s.s., has its sculpture confined to the beaks, and the anterior adductor and retractor muscle scars almost invariably separate; *Protohyridella* has a strong shell sculpture, separate anterior adductor and retractor scars, and is of small size; *Echyridella* is of variable facies but has beak sculpture only, separate anterior adductor and retractor scars, very heavily developed siphons, and an anterior extension of the labial palps; *Nesonaia* has a very strongly developed hinge and the sculpture tends to be developed down the sides and posterior slope of the shells as fine wrinkles.

Relationships

The genus *Hyridella* is the only member of the subfamily recognized here. *Hyridella* is known as a fossil: *H. wilkinsoni* (Etheridge Jr.) from the Pliocene of New South Wales and Victoria, and *H. whitecliffsensis* (Newton) from the Cretaceous, New South Wales.

Subgenus HYRIDELLA Swainson

Hyridella Swainson, 1840, pp. 285 and 380. Type species by monotypy: *Unio australis* Lamarck, 1819.

Leiovirgus Haas, 1912, p. 132. Type species by original designation: *Unio misoolensis* Schepman, 1897.

Propehyridella Cotton & Gabiel, 1932, p. 158. Type species by original designation: *Unio nepeanensis* Conrad, 1850.

Hyridunio Iredale, 1934, p. 68. Type species by original designation: *Hyridunio australis drapeta* Iredale, 1934.

Rugoshyria Iredale, 1934, p. 71. Type species by original designation: "*Unio paramattensis* Lea, 1862 = *Unio depressa* Lamarck, 1819".

Diagnosis

Shell Characters.—Freshwater mussels of the genus *Hyridella* of small to medium size reaching about 100 mm in length. Shells tending to be elongate, MHI about 55 per cent., not usually winged, BHI about 85 per cent., of unionine facies; hinge strong, unionid, rarely reduced; cardinal teeth usually erect, grooved; sculpture limited to ridges on the beaks, ridges usually V-shaped, tending to separate below; shell substance typically relatively heavy; anterior muscle scars firmly impressed, retractor and adductor almost invariably separate, retractor scar a deep pit beneath cardinal teeth.

Anatomy.—With the general characters of the genus; siphons prominent but not heavily developed; gill diaphragm of medium length, perforate.

Glochidium.—Subtriangular, hooked, about 250μ in hinge plane, 240μ deep (Fig. 13).

Distribution

Eastern Australia, south of the Tropic of Capricorn; Tamar River system of Tasmania; North and South Islands of New Zealand (rare); south-western New Guinea.

Differential Diagnosis of Species

The six species assigned to this subgenus may be separated thus: *Hyridella* (*Hyridella*) *aucklandica* (Gray), from New Zealand, has an MHI of 45–50 per cent. and a sinuate ventral margin; *H.* (*H.*) *misoolensis* from New Guinea is similar in form but tends to taper posteriorly; *H.* (*H.*) *australis* (Lam.) is typically oblong-ovate in shape, with a prominent posterior ridge, heavy beak sculpture and MHI about 60 per cent.; *H.* (*H.*) *drapeta* (Iredale) is elongate oval, with a flattened posterior ridge, slightly winged, MHI about 55 per cent. and with delicate beak sculpture; *H.* (*H.*) *depressa* (Lam.) is relatively more elongate, MHI about 50 per cent., and the dorsal margin anterior to the beaks slopes away markedly; *H.* (*H.*) *narracanensis* (Cotton & Gabriel) has a very characteristic amygdaloid shape, is small and possesses a very strong hinge.

Relationships

The subgenus is closely related to the subgenera *Echyridella*, *Protohyridella*, and *Nesonaia* to all of which it was probably ancestral.

Hyridella (Hyridella) australis (Lamarck)

Plate 9, Figs. 6–18; Plate 10, Figs. 1–6; Plate 17, Fig. 1.

Unio australis Lamarck, 1819, p. 80. Hanley, 1843,* p. 192, pl. 21, fig. 25. (?) Philippi, 1848, p. 81, *Unio* pl. v, fig. 5.

Unio depressa Lamarck, Lesson, 1831, pp. 427–8, pl. 15, figs. 5 and 5*A*. (Non *U. depressa* Lamarck 1819.)

Unio napeanensis (*sic*) Conrad, 1850, p. 10; 1854, p. 296, pl. 26, fig. 4. Reeve, 1865, pl. xxiii, sp. and fig. 110. *U. nepeanensis* (*sic*) Conrad, Smith, 1881, p. 312. Tate and Brazier, 1882, p. 568.

*The text of Hanley's Catalogue was published in 1843, the plates in 1856.

Unio dorsuosus Gould, 1851, p. 296; 1852, p. 430; 1856, pl. 37, figs. 540, 540*a*, and 540*b*.
Unio lessoni Kuster, 1856, p. 135, pl. xxxvii, fig. 4. (New name for *U. depressa* Lam. of Lesson, 1831.)
Diplodon (*Hyridella*) *dorsuosus* (Gould), Simpson, 1914, p. 1289.
Diplodon (*Hyridella*) *lessoni* (Kuster), Simpson, 1914, p. 1296.
Propehyridella nepeanensis (Conrad), Cotton and Gabriel, 1932, p. 158, pl. xvi, fig. 5. Iredale, 1934, pp. 73–4, pl. v, fig. 11, pl. vi, fig. 11; 1943*a*, p. 190; 1943*b*, pp. 91–2, fig. 1. Gabriel, 1939, pp. 131–2, pl. iv, fig. 40. McMichael, 1952, p. 399, text fig. p. 400.
Propehyridella nepeanensis opportuna Iredale, 1934, p. 74, pl. v, fig. 12, pl. vi, fig. 12; 1943*a*, p. 190.
Propehyridella nepeanensis narracanensis Cotton & Gabriel, Iredale, 1934 (in part), p. 74 (not pl. v, fig. 13, nor pl. vi, fig. 13); 1943*a*, p. 190. (Non *P. narracanensis* Cotton & Gabriel, 1932.)
Propehyridella nepeanensis novata Iredale, 1943*b*, p. 92.
Hyridella australis (Lamarck), McMichael, 1955, pp. 6–13. Kershaw, 1956, p. 53.

Remarks

The identity of *Unio australis* Lamarck has been established with certainty only recently (McMichael 1955). Prior to this, the name was variously applied, but principally to *Velesunio ambiguus* (Phil.). For the present species, the name *Unio nepeanensis* Conrad (or a junior synonym) has generally been used.

Both Hanley (1843) and Philippi (1848) figured what they believed to be *U. australis* Lam., but the figures are inadequate to permit accurate identification. Smith (1881) interpreted Philippi's figure as representing *Velesunio ambiguus*, but since it is possible that it may represent the present species (see McMichael 1955, p. 6), it is included, doubtfully, in the synonymy above.

Lesson (1831) reported on a shell collected from the Nepean River, New South Wales, by members of the "Coquille" expedition and used the name *Unio depressa* Lam. for it; it was in fact a corroded specimen of *U. australis*. Kuster (1856) realized that it was not *U. depressa* Lam. and believing it to be unnamed, provided a new name, *Unio lessoni*, for it. In this he was anticipated by Conrad (1850, 1854), who again named the species and noted that Lesson's *U. depressa* was the same.

Conrad (1850) received specimens from the Nepean River and named them *Unio napeanensis*, mis-spelling the river name. He noted later (1854) that his species was the same as *U. depressa* Lesson 1831, but pointed out that *U. depressa* Lam., as figured by Delessert and Chenu, was very different. Conrad's figure and description were good, and since *Unio australis* was unrecognizable at this time, Conrad's name became applied to the species.

Wilke's narrative of the United States Exploring Expedition suggests that the shell described as *Unio dorsuosus* by Gould (1851) probably came from the Nepean River. The exact locality was lost and the shell incorrectly marked "Fiji". Gould suspected an error and gave "Eastern Asia" as the possible locality. In a later work, Gould (1862*b*) recognized that his species was a synonym of *U. nepeanensis* Conrad, but Simpson (1914) used Gould's name in preference to Conrad's, through an error in dating Conrad's paper.

Cotton and Gabriel (1932), still using *Hyridella australis* (Lam.) for *Velesunio ambiguus*, named *Unio nepeanensis* Conrad as the type of their genus *Propehyridella*.

Iredale (1934) identified a species occurring near Sydney as *U. australis* Lam., placing it in a new genus *Hyridunio*. He selected a new subspecies, *drapeta*, from Queensland, as type "in order that there can be no mistake in the genus proposed". His choice was incorrect and the species selected by him must now bear the name *Hyridella drapeta* (Iredale). He continued to use *U. nepeanensis* for the present species, regarding it as polytypic, recognizing two subspecies and later (1943*b*) a third. The typical form was considered to occur in streams near Sydney. Shells from the Richmond River, which were larger and longer, were named *Propehyridella nepeanensis opportuna*. Shells from the Mitchell River, Victoria, were regarded as a southern subspecies for which Iredale used the name *narracanensis* Cotton & Gabriel, 1932, originally proposed as a full species of *Propehyridella*. Though Iredale's shells were relatively large and the type of *narracanensis* small, Iredale believed *narracanensis* to be the juvenile of his Victorian subspecies of *nepeanensis*. Though the type of *narracanensis* is a juvenile, it represents a distinct species occurring in Victoria and Tasmania. (Iredale named the Tasmanian representatives *Rugoshyria depressa sodalis*.) In 1943, Iredale named some shells, more elongate than typical *nepeanensis*, *Propehyridella nepeanensis novata*, the locality being the Upper Bellenger River, New South Wales. Examination of the type series reveals that the holotype is a fairly typical *H. australis* while the paratype is a juvenile *H. depressa*. These subspecies recognized by Iredale seem to represent local populations in different and isolated rivers. The forms may be ecotypes or only ecophenotypes, but are not admitted here as true geographic subspecies.

Types

Unio australis Lamarck: The type series consists of two shells in the Muséum National d'Histoire Naturelle, Paris. The larger shell, for which Lamarck gave the dimensions, has been selected as lectotype (McMichael 1955). The type locality given by Lamarck was "Nouvelle-Hollande". Cotton and Gabriel (1932, p. 156) selected South Creek, near Sydney, as the type locality, basing their selection on some specimens of *Velesunio ambiguus* sent by Dr. Cox, labelled "*Unio australis* Lamarck from South Creek near Sydney where Lamarck's types were first secured". To our knowledge, *H. australis* does not occur in South Creek, and since members of the "Géographe" expedition visited the Nepean River, this is selected as restricted type locality.

Unio nepeanensis Conrad: Holotype ANSP Mus. No. 129955. Paratype MCZ Reg. No. 72077. Type locality: Nepean R., N.S.W.

Unio dorsuosus Gould: Holotype USNM, Reg. No. 5925. Type locality: Given by Gould as "Eastern Asia?", specimen marked "Fiji". Here restricted, Nepean R., N.S.W.

Unio lessoni Kuster: USNM, Reg. No. 85723. Is specimen figured by Lesson (1831). Type locality: Nepean R., N.S.W.

Propehyridella nepeanensis opportuna Iredale: Holotype AM Reg. No. C. 61983. Paratypes AM Reg. No. C. 61984. Type locality: Creek at Booyong, Richmond R., N.S.W.

Propehyridella nepeanensis novata Iredale: Holotype AM Reg. No. C. 61982. Type locality: Upper Bellenger R., N.S.W.

Description

Shell Morphology.—Shells fairly large, reaching a maximum length of about 90 mm, MHI 56–61 per cent. Outline oblong-ovate, anterior portion of shell well developed, BLI about 30 per cent. Anterior margin uniformly rounded, ventral margin slightly curved in young shells, rather straight in older specimens, sometimes slightly sinuate; dorsal margin slightly elevated, posterior to beaks, shell only slightly

winged, BHI about 87 per cent.; posterior margin almost squarely truncate in young specimens, less acutely so in larger ones; postero-ventral margin rounded. Shell usually swollen, especially along posterior ridge; posterior slope a little compressed; beaks swollen, slightly elevated, and strongly sculptured with V-shaped ridges, separating ventrally, the posterior member of each V being heavier and more raised.

Periostracum in young specimens deep olive-brown, becoming deep purple-brown and always shiny; marked by fine growth lines and in young shells a faint series of concentrically arranged striations apparently developed as a continuation of the beak sculpture. Nacre silvery white, stained bluish pink below the beaks and variously stained elsewhere with copper and yellow coloured blotches. Shell substance solid, even in young specimens; thickened near the antero-ventral border.

Hinge strong, unionid; cardinal teeth erect, solid, usually grooved and denticulate, often pointed, the left sometimes recurved at the tip; lateral teeth strong, thick and blunt anteriorly, expanding and sharpening posteriorly.

Posterior muscle scars lightly impressed, anterior scars firmly impressed, retractor scar cutting deeply beneath cardinal tooth; beak muscle scars a series of deep pits in the beak cavity. Pallial line weakly impressed except anteriorly in older shells.

Fig. 13.—Free glochidium of *Hyridella* (*H.*) *australis* (Lam.), Williams River, Dungog, N.S.W.

Anatomy.—With the characters of the genus. Siphons of medium size, well defined and prominent in living specimens, branchial siphon about 1½ times size anal, both pigmented evenly deep red-brown to black; branchial bears 1–2 rows medium sized, paler papillae internally. Gills often red-brown in colour; outer triangular and attached only by dorsal border to mantle; inner gill more elongate, attached to foot dorsally and to mantle and foot posteriorly. Palps small, triangular, pointed at free apex; outer palp united with mantle at its middle. Gill diaphragm elongate and perforate. Marsupium occupies middle third of inner gill of females. Outer gill of both sexes looped with regularly spaced interlamellar junctions which represent fusions of long, thin-walled interfilamentar junctions. Discrete blood vessels few, large sinuses plentiful. Inner gill of female similar to above in non-marsupial region, with more frequent interlamellar junctions. Marsupium with closely packed interlamellar junctions, frequently discontinuous and short with only middle sector possessing folded walls, dense connective tissue and well-developed muscle strands; inner section of junctions expanded as large blood sinuses.

Chitinous supporting rods heavy and frequently discontinuous.

Glochidium.—Subtriangular, hooked, 250μ in hinge plane, 240μ deep (Fig. 13).

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Unio australis Lectotype	53	13	25%	31	59%	25	81%	20
U. australis Paratype	48	12	25%	29	60%	24	83%	15
U. nepeanensis Holotype ex Conrad	48	13	27%	30	63%	26	87%	17
U. nepeanensis Paratype MCZ	49	13	26%	29	59%	25	86%	18
U. dorsuosus Holotype	39	11	28%	22	56%	19	86%	13
U. lessoni Holotype ex photo. USNM	61	15	25%	38	62%	32	84%	26
P. nepeanensis opportuna Holotype	68	15	22%	39	57%	33	85%	28
P. nepeanensis novata Holotype	41	10	24%	24	58%	21	88%	14
Mean 4 specimens, Brogo R., Bega; AM	86	23	27%	50	58%	45	90%	35
Mean 5 specimens, Woronora R.; AM	64	17	27%	37	58%	32	86%	25

Material Examined

Specimens as above and from QUEENSLAND: Waraba Ck., Caboolture. NEW SOUTH WALES: Tweed R., Murwillumbah; Upper Manning R.; Upper Hastings R.; Charity Ck., near Taree; Woronora R., Heathcote; Salamanca R.; George's R., Liverpool; Brogo R., Bega; Nepean R., Penrith, Camden, Douglas Park; Williams R., Dungog. VICTORIA: Mitchell R., Bairnsdale; Barwon R., Winchelsea; Glengarry R.; Yarra R.

Range

Coastal rivers of eastern Australia, from Caboolture, Queensland, south to Yarra River, Victoria (Fig. 14).

HYRIDELLA (HYRIDELLA) DRAPETA (Iredale)

Plate 10, Figs. 7–13; Plate 16, Fig. 13; Plate 18, Figs. 4 and 5

Hyridunio australis drapeta Iredale, 1934, pp. 68–9, pl. v, fig. 2, pl. vi, fig. 2.
Hyridunio australis (Lamarck), Iredale, 1934, p. 69, pl. v, fig. 1, pl. vi, fig. 3. McMichael, 1952, p. 400, figure in text. (Both non *U. australis* Lam.)
Hyridunio australis orion Iredale, 1934, p. 69.
Hyridunio renutus Iredale, 1934, pp. 69–70, pl. v, fig. 3, pl. vi, fig. 4.
Hyridunio australis casus Iredale, 1943*b*, p. 90, fig. 1 in text.
Hyridella drapeta (Iredale) McMichael, 1955, p. 12. Kershaw, 1956, p. 53.
Hyridella drapeta orion (Iredale), Kershaw, 1956, p. 53.
Hyridella renutus (Iredale), Kershaw, 1956, p. 53.

Remarks

This species, in shape, is more or less intermediate between *H. australis* and *H. depressa*, but differs constantly from them both. Prior to 1934, it was probably confused with them, having a somewhat similar distribution. It was included by Cotton and Gabriel (1932) in their complex *Propehyridella cultelliformis*, but it is noticeably different from that species. Iredale's (1934) use of the name *Hyridunio australis* for it is the first which can be assigned definitely to this species, and Iredale was the first to figure it.

Iredale selected the present species as *Unio australis* because it occurred near Sydney, matched Lamarck's (1819) brief description and resembled Hanley's (1843) figure, though this is so small as to be almost useless. He recognized three forms: (1) the "typical" "*australis*" from central coastal New South Wales, (2) a more elongate form from South Queensland which he named *H. australis drapeta* and designated type species for the genus *Hyridunio*, and (3) a smaller, less winged form from Victoria which he named *H. australis orion*.

Fig. 14.—Distribution of subfamily Hyridellinae: *Hyridella* (*H.*) *australis* and *H.* (*H.*) *drapeta* (same distribution).

Since this species has proved not to be *Unio australis* Lamarck, it must take the next available name, which is *drapeta* Iredale. The invalidity of the generic name *Hyridunio* Iredale has already been discussed; it falls as a junior subjective synonym of *Hyridella* Swainson. This present species, therefore, becomes *Hyridella* (*Hyridella*) *drapeta* (Iredale). The subspecies recognized by Iredale are not accepted here, *H. australis orion* being considered a synonym of *drapeta*.

Iredale (1934) named an additional species, *Hyridunio renutus*, based on a single specimen from the Latrobe River, Victoria, admitting that it might be an abnormal specimen. We agree with this latter view, as other shells from the Latrobe River at Maryvale, in the National Museum, Melbourne, are quite normal.

Iredale (1943*b*) admitted a fourth subspecies for "*Hyridunio australis*", shells from the Clarence River, New South Wales, being less winged and a little more elongate than the typical form. These were named *H. australis casus*, but they are not taxonomically separable from typical *H. drapeta*.

Though the subspecies admitted by Iredale differ somewhat from typical *drapeta*, the species is regarded here as being monotypic, the various forms being considered ecotypes or ecophenotypes. In southern Queensland, for example, elongate forms are common near Brisbane, yet several populations from streams in the vicinity are shorter and closely resemble Victorian forms. Similarly, the Clarence River population ("*H. australis casus*") is quite close to some Victorian forms, suggesting that they are merely ecotypes.

Types

Hyridunio australis drapeta Iredale: Holotype AM Reg. No. C. 61934. Paratype AM Reg. No. C. 61935. Type locality: Brisbane R., Qld.

Hyridunio australis orion Iredale: Lectotype (here selected) AM Reg. No. C. 61931. Paratypes AM Reg. No. C. 61932. Type locality: Tomahawk Brook, near Lilydale, Vic.

Hyridunio renutus Iredale: Holotype AM Reg. No. C. 61936. Type locality: Latrobe R., Gippsland, Vic.

Hyridunio australis casus Iredale: Holotype AM Reg. No. C. 61938. Paratypes AM Reg. No. C. 61939. Type locality: Clarence R. at Tucavia, N.S.W.

Description

Shell Morphology.—Shells elongate oval, of medium size; maximum length about 90 mm, MHI about 55 per cent. Anterior portion of shell relatively short, BLI about 22 per cent. Anterior margin evenly but bluntly rounded, ventral margin straight or sinuate in the middle; dorsal margin sloping away anterior to beaks, elevated posterior to beaks then falling off ventrally in a gentle curve; posterior end bluntly curved. Some shells appear quite winged, BHI about 85 per cent.

Periostracum dark brown to black, dull and smooth, marked only by fine growth lines. Nacre bluish white, stained copper, or coppery purple, in beak cavities, copper blotches elsewhere. Shell substance relatively heavy, thick at the antero-ventral border.

Shell slightly swollen, anterior end compressed, posterior end inflated, with a shallow but definite sulcation separating the anterior and posterior ends of the shell; posterior ridge flattened. Beaks low, not swollen, usually corroded. In perfect young shells, beaks are sculptured with a series of V-shaped ridges, the dorsal pair joined as a V, the others incomplete, the posterior members continuing for some distance down the posterior ridge (Plate 16, Fig. 13). In older shells, only shallow ridges remain, confined to the beaks.

Hinge strong, unionid; cardinal teeth very heavy and erect; in right valve, tooth paired, heavily grooved on internal faces, deeply serrated on outer edge; in left valve, single tooth often with a deep pit, grooved internally, serrated at the edge. Lateral teeth relatively long, slightly curved, blade-like, often slightly serrated.

Anterior muscle scars strongly impressed, retractor and adductor separate, retractor forming a deep pit beneath the cardinal tooth; posterior scars lightly impressed. Beak muscle scars several, in a row, under the beaks. Pallial line prominent, particularly anteriorly.

Anatomy.—With the characters of the genus. Siphonal region deeply pigmented brown, splotched with black; pigment extending well down to ventral border of mantle. Siphons moderately large, prominent, branchial hardly bigger than anal; branchial siphon with papillae, commencing as a single row ventrally, giving rise to a criss-cross pattern dorsally, the inner series larger. Diaphragm long, with a minute perforation. Outer gills small, triangular; inner gills more elongate, attached to foot and mantle anteriorly. Palps small, triangular. Marsupium occupies middle third of inner gills of females. Male gills usually deep brown in colour, female gills, especially inner, creamy white. Outer gill in both sexes looped, with regularly spaced, weakly developed interlamellar junctions. Interfilamentar junctions irregular and very thin-walled, enclosing spacious blood sinuses. Inner gill of female in non-marsupial region as above. Marsupium with many interlamellar junctions, mostly discontinuous, with folded walls, epithelium frequently ciliate, possessing many loosely packed muscle fibres; connective tissue diffuse and characteristically with a large blood sinus at each end. In a near gravid gill the marsupium is distended, the interlamellar junctions being long and thin, and more widely spaced, dividing the marsupium into a series of rectangular compartments packed with embryos. Chitinous rods heavy and discontinuous (Plate 18, Figs. 4 and 5).

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
H. australis drapeta								
Holotype	82	17	21%	40	49%	36	90%	25
H. australis orion								
Lectotype	79	17	22%	44	56%	38	86%	25
H. renutus								
Holotype	73	16	22%	47	64%	38	81%	23
H. australis casus								
Holotype	73	18	25%	36	49%	33	91%	23
Mean 5 specimens, Manning R. at Wingham; AM	66	15	23%	37	56%	32	87%	21
Mean 5 specimens, Cann R., Vic.; MCZ	69	16	23%	38	55%	33	87%	22
Mean 17 specimens, North Pine R., near Brisbane; ZDQ	76	17	22%	39	51%	32	82%	23
Mean 8 juveniles, Caboolture, F.S. Colliver collection	30	9	30%	16	53%	14	87%	8

Material Examined

As above and from QUEENSLAND: North Pine R.; Blunder Ck.; Kedron Brook; Oxley Ck. (all near Brisbane); Currumbin Ck.; Logan R., Pimpama; Waraba Ck., Caboolture, Elimbah; Tibrogargan Ck., Beerwah. NEW SOUTH WALES: Allyn R.; Clarence R., Copmanhurst, Tucavia; Byangum R.; Bogan R.; Hunter R.; Richmond R.; Bangalow Ck., Byron Bay; Warrel Ck. (tributary of Nambucca R.), Eungai; Manning R., Mt. George, Wingham; Stroud Ck.; Nepean R., Richmond, Camden. VICTORIA: Barwon R., Birregurra; Mitchell R., Bairnsdale; Cockatoo Ck.; Latrobe R., Maryvale; Panton Hills, near Melbourne; Glengarry R., Longford; Tomahawk

Brook, near Lilydale; Bunyip R.; Tarra R., Tarraville, Port Albert; Fraser Ck., Wilson's Promontory; Mordialloc Ck.; Broken R., Nalinga; Erskine R.; Yarra R., Woori Yallock, Watson's Ck.; Narracan R.; Swamp near Sale; Tarwin R., Inverloch; Cann R., Cann River; Sealer's Ck., Wilson's Promontory; Creek near Mt. Evelyn.

Range

Coastal rivers of southern Australia, from Caboolture, Queensland, to rivers of Victoria, west of Port Phillip Bay (Fig. 14).

Hyridella (Hyridella) depressa (Lamarck)

Plate 11, Figs. 1–11; Plate 12, Figs. 1–6

Unio depressa Lamarck, 1819, p. 79. Delessert, 1841, pl. 12, fig. 5. Conrad, 1854, p. 295, pl. 26, fig. 2 (copy of Delessert's figure). Smith, 1881, p. 308.
Unio cultelliformis Conrad, 1850, p. 10.
Unio sp., Conrad, 1854, p. 296, pl. 26, fig. 6.
Unio mutabilis Lea, 1859, p. 152; 1860, p. 248, pl. 38, fig. 127. Reeve, 1865, pl. 24, sp. and fig. 112.
Unio paramattensis (*sic*) Lea, 1862, p. 176; 1866, p. 60, pl. 20, fig. 59.
Diplodon (*Hyridella*) *cultelliformis* (Conrad), Simpson, 1914, p. 1300.
Diplodon (*Hyridella*) *mutabilis* (Lea), Simpson, 1914, p. 1308.
Propehyridella cultelliformis (Conrad), Cotton and Gabriel, 1932 (in part), p. 159, pl. xvi, fig. 6. Gabriel, 1939 (in part), p. 132, pl. iv, fig. 41.
Rugoshyria depressa (Lamarck), Iredale, 1934, pp. 71–2, pl. v, fig. 6, pl. vi, fig. 6. McMichael, 1952, p. 400, text fig. p. 400.
Rugoshyria depressa monticola Iredale, 1934, p. 72, pl. v, figs. 7*a*, 7*b*, pl. vi, fig. 10.
Rugoshyria depressa vicinalis Iredale, 1934, p. 72.
Rugoshyria cultelliformis (Conrad), Iredale, 1934, p. 73, pl. v, fig. 10, pl. vi, fig. 7.
Rugoshyria depressa bega Iredale, 1943*b*, p. 91.
Rugoshyria depressa lowanna Iredale, 1943*b*, p. 91, text fig. 1.
Hyridella vicinalis (Iredale), Kershaw, 1956, p. 54.
Hyridella depressa (Lamarck), McMichael, 1957, p. 241.

Remarks

Lamarck's description of *Unio depressa* was brief, but Delessert's figure, though of a juvenile, was good and the species can be identified easily. A few authors, including Lea, have misidentified it and several additional names for the species have appeared. Reeve (1864) possibly added confusion by figuring a specimen of *Velesunio legrandi* from Tasmania under the name *depressa*.

Conrad (1850) gave the name *cultelliformis* to a specimen from the Bogan River, New South Wales, but later (1854) synonymized his species under *depressa* and reproduced Delessert's original figure of *depressa* to illustrate it. At the same time, Conrad figured a shell (1854, pl. xxvi, fig. 6) from the Bogan River, listed (loc. cit., p. 296) as "*Unio* sp.". The shell was undoubtedly a *depressa* and may have been the holotype of *cultelliformis*. Why it was listed as "*Unio* sp." is difficult to explain. Iredale (1934) misunderstood the plate: believing the larger figure (fig. 6) to be typical *paramattensis* Lea (= *depressa* Lam.), he assumed Conrad's type of *cultelliformis* to be different and thereafter used the name *cultelliformis* for shells from "central and northern Australia" though, to our knowledge, the group does not occur there. The shell figured by Iredale to illustrate this particular species was from

an unknown locality. It seems certain that *U. cultelliformis* Conrad is correctly synonymized with *H.* (*H.*) *depressa*.

Lea (1859) named a series of shells *Unio mutabilis*, having specimens from three localities. One (Cuming collection) was localized as "Brisbane Water, Australia", another (Cuming collection) was from New Zealand, a third was labelled "Murray River, Australia" while a fourth, a juvenile, was unlabelled. Lea claimed that his description and figure were of the New Zealand shell, but while it has some resemblance to the New Zealand *Hyridella menziesi*, the figured specimen is definitely *Hyridella depressa*. The locality, in keeping with Cuming's methods, is probably incorrect. The Brisbane Water specimen was figured by Reeve (1865) and, though the shell is distorted, is presumably this species. It is figured here, Plate 11, Fig. 11. Brisbane Water is an estuary of the Hawkesbury River, near Sydney, and since the Nepean River flows into the Hawkesbury, the locality is acceptable. The "Murray River" shell, which is in the USNM, is a typical *depressa*, but the species, to our knowledge, does not occur in this river; the locality may be again incorrect.

Lea (1862) named a further form of this species from the Parramatta River *Unio paramattensis* (*sic*), the type in the USNM confirming its true identity as *depressa*.

Simpson (1900, 1914), Cotton and Gabriel (1932), and Gabriel (1939) used Conrad's name, *cultelliformis*, for the present species, claiming that the name *Unio depressa* Lam. was invalidated for this species by *Mya depressa* Donovan, a species which was later transferred to *Unio*. None of the above authors, however, listed the present species under either *Mya* or *Unio*.

Iredale (1934) correctly synonymized *U. mutabilis* and *U. paramattensis* with *depressa* but, as outlined above, separated *cultelliformis*. He erected a new genus, *Rugoshyria*, for these shells, the present species being the type of the genus. As with *Hyridella australis*, Iredale admitted a number of subspecies of *depressa*, three in 1934 and a further two in 1943. One of these subspecies, *Rugoshyria depressa sodalis*, was named for a figure by May (1923) of a Tasmanian shell, but that form is considered to be *Hyridella narracanensis* (Cotton & Gabriel) and is discussed under that heading. The other subspecies, after close examination and comparison with large series of *H. depressa*, are considered to be ecotypes or ecophenotypes only, and they are confined to single rivers. In other words, *H. depressa* is considered a variable but monotypic (in the nomenclatural sense) species.

Types

Unio depressa Lam.: Holotype MNHN Reg. No. ? Type locality: "rivers of New Holland"; here restricted, Nepean R., near Sydney.

Unio cultelliformis Conrad: Holotype ANSP Reg. No. 129954. Type locality: Bogan R., N.S.W. (The late Dr. Pilsbry informed us (9.xii.54) that this shell could not be located.)

Unio mutabilis Lea: Holotype was in the Cuming collection which is now in the BM. The specimen figured by Reeve is the Brisbane Water specimen. The Reeve specimen has its tablet marked, in Lea's handwriting, "*M. mutabilis* Lea, New Zealand, H. Cuming. (I kept one of these specimens)". A paratype, USNM Reg. No. 85615, is labelled New Zealand, and is presumably the shell mentioned by Lea. It is also probably the juvenile, from an unknown locality, mentioned by Lea. A second paratype, USNM Reg. No. 84405, is the "Murray R." specimen. The type locality cannot be determined accurately.

Unio paramattensis Lea: Holotype USNM Reg. No. 84405. Paratype MCZ Reg. No. 17015. Type locality: Parramatta R., Parramatta, N.S.W.

Rugoshyria depressa monticola Iredale: Holotype AM Reg. No. C. 61952. Paratype AM Reg. No. C. 79. Type locality: Grosse's Plain Creek, Moonbar Run, Mt. Kosciusko, N.S.W.

Rugoshyria depressa vicinalis Iredale: Syntypes AM Reg. No. C. 57939. The largest specimen, figured here (Plate 12, Figs. 1 and 2), is here selected as lectotype. Type locality: Mitchell R., Bairnsdale, Vic.

Rugoshyria depressa bega Iredale: Holotype AM Reg. No. C. 43362. Paratypes AM Reg. No. C. 43362. Type locality: Tantawanglo R., tributary of Bega R., N.S.W.

Rugoshyria depressa lowanna Iredale: Holotype AM Reg. No. C. 61950. Paratypes AM Reg. Nos. C. 61951 and C. 61966. Type locality: Little Nymboida R., Dorrigo, N.S.W.

Fig. 15.—Distribution of subfamily Hyridellinae (*continued*): *Hyridella* (*H.*) *depressa*.

Description

Shell Morphology.—Shell small but elongate, maximum length about 70 mm, MHI about 50 per cent. Anterior portion of shell relatively short, BLI about 20 per cent. Anterior margin evenly rounded, ventral margin straight for most of its length, then curving gently up to meet posterior margin; dorsal margin anterior to beaks sloping markedly, elevated posterior to beaks, producing some degree of winging, BHI about 80 per cent., then obliquely truncate; postero-ventral margin rounded, somewhat produced. Shell slightly swollen posteriorly, posterior ridge well developed, posterior slope compressed. Beaks not swollen, depressed, sculptured strongly with V-shaped ridges, rarely extending on to shell.

Periostracum dark brown to black, relatively shiny, marked by fine growth lines. Nacre bluish or bluish white, iridescent posteriorly, stained with copper coloured spots. Shell substance variable, typically thick.

Hinge strong, unionid; cardinal tooth double in right valve, erect, grooved and serrated, lower tooth the larger; cardinal tooth single in left valve with either a deep, grooved pit or having the appearance of a second accessory tooth posteriorly; lateral teeth moderately long and curved. Some specimens have weak teeth, with cardinals almost lamellar.

Anterior muscle scars deeply impressed, retractor separate from adductor and forming a deep pit beneath the cardinal teeth; posterior scars weakly impressed. Beak muscle scars scattered in beak cavity.

Anatomy.—With the characters of the subgenus. Siphons well developed, prominent, and evenly pigmented. Anal siphon separated from branchial by a marked mantle bridge, 3–4 mm long. Branchial siphon about 1½ times size anal and possessing up to 5 rows of closely set papillae, some dendritic, on inner face. Gill diaphragm long, perforation minute. Outer gill triangular, free except on dorsal border. Inner gill more elongate. Palps small, triangular; outer palp attached to mantle for about one-third of its outer face, dorsally. Marsupium occupies middle third of inner gill of females. Outer gill in both sexes looped, with fairly regular interlamellar junctions usually weakly developed. Interfilamentar junctions long, typically thin-walled, blood vessels few, sinuses large. Inner gill of females in non-marsupial region as above. Marsupium with many interlamellar junctions, usually discontinuous, with fairly dense connective tissue, well-developed muscle strands and typically with a sinus at each end. Chitinous supporting rods heavy, mostly discontinuous.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. depressa Holotype, ex photo.	53	12	23%	27	51%	23	85%	12
U. cultelliformis Holotype ex Conrad	50	11	22%	26	52%	21	81%	14
U. mutabilis Holotype ex Lea	55	10	18%	24	44%	19	79%	13
U. mutabilis Paratype USNM	33	8	23%	17	51%	14	82%	10
U. mutabilis Paratype BM	76	19	25%	33	43%	30	90%	22
U. paramattensis Holotype	58	14	23%	30	52%	25	81%	18
U. paramattensis Paratype	48	10	21%	24	50%	20	83%	15
R. depressa monticola Holotype	50	10	20%	29	58%	24	83%	16
R. depressa monticola Mean 4 paratypes	47	10	21%	26	55%	22	84%	14
R. depressa vicinalis Lectotype	65	15	23%	33	53%	28	85%	20
R. depressa bega Holotype	68	12	18%	32	46%	26	81%	20
R. depressa lowanna Holotype	59	10	17%	28	47%	23	82%	16
Mean 5 specimens, Nepean R.; AM	58	11	19%	28	48%	24	86%	14
Mean 10 specimens, Elimbah; ZDQ	47	11	23%	24	51%	18	75%	12

Material Examined

As above and from NEW SOUTH WALES: Richmond R., Casino, Booyong Ck.; Woronora R., Heathcote; Waterfall; Manning R., Mattagonali, Mt. George; George's R., Liverpool; Hunter R.; Clarence R.; Bong Bong Ck., Bowral; Nepean R., Wallacia, Picton; Salamanca R.; South Ck., near Sydney; Fishpond Ck., near Hornsby; Berowra Ck., near Hornsby; Parramatta R., Parramatta. VICTORIA: Mitchell R., Bairnsdale; Narracan R.; Erskine R., near Lorne. QUEENSLAND: Waraba Ck., Elimbah, near Caboolture.

Range

Coastal rivers of eastern Australia from Caboolture, Queensland, south to the eastern rivers of Victoria (Fig. 15).

HYRIDELLA (HYRIDELLA) NARRACANENSIS (Cotton & Gabriel)

Plate 12, Figs. 7–12; Plate 18, Fig. 3

Unio spp. Johnston, 1889, pp. 95–6, pl. 1, figs. 1, 2, 3, 4, 5, 8, and 8*a*, pl. 2, fig. 12.
Diplodon mortonicus (*sic*) (Reeve) May, 1923, p. 23, pl. 9, fig. 12. (Non *Unio moretonicus* Reeve 1865.)
Propehyridella narracanensis Cotton & Gabriel, 1932, p. 159, pl. xvi, fig. 8. Gabriel, 1939, p. 133, pl. iv, fig. 42.
Rugoshyria depressa sodalis Iredale, 1934, p. 72.
Propehyridella nepeanensis narracanensis Cotton & Gabriel, Iredale, 1934 (in part), p. 74, pl. v, fig. 13, pl. vi, fig. 13.
Hyridella narracanensis Cotton & Gabriel, Kershaw, 1956, p. 54.

Remarks

The species here referred to under this name is an easily recognizable form, previously known and understood from Victoria but not from Tasmania where it also occurs. The holotype is a juvenile shell and not typical, but some of the paratypes give a better concept of the species.

Johnston (1889), in an account of the variability of Tasmanian mussels, figured two quite distinct forms, typical *Velesunio legrandi* (Petterd) and the present species, recognizing neither as other than variants of the local "species".

May (1923) figured a specimen of the present species under the name *Diplodon mortonicus* (Reeve), but the name cannot possibly apply. Iredale (1934) thought that May's figure represented a subspecies of *Rugoshyria depressa* (= *Hyridella depressa*) and named it *R. depressa sodalis*, the figured specimen being, therefore, the holotype. On the other hand, shells from Mt. Kosciusko which Iredale named *R. depressa monticola* and claimed to be closely related to *sodalis* belong with *H. depressa* and not here.

Iredale (1934) used *narracanensis* as a subspecific name for Victorian populations of *Hyridella australis*, believing the present species to be the juvenile. The juvenile shell which Iredale figured was a topotype of *narracanensis* and is therefore included in the synonymy, but adult shells included by Iredale in the subspecies belong with *H. australis* and not here.

Types

Propehyridella narracanensis Cotton & Gabriel: Holotype NMV Reg. No. F. 629 (old number 71237). Paratypes* NMV Reg. No. F. 13135. Type locality: Narracan R., Thorpdale, Gippsland, Vic.

Rugoshyria depressa sodalis Iredale: Holotype is specimen figured by May (1923), which cannot be located.

Description

Shell Morphology.—Shells small, maximum length about 60 mm, MHI about 55 per cent. Shell outline amygdaloid; anterior portion of shell relatively short, BLI 20–25 per cent. Anterior margin somewhat truncate but evenly rounded; dorsal margin slightly elevated immediately posterior to beaks, BHI about 85 per cent., then very obliquely truncate; ventral margin usually convex, rarely straight, then curving upwards posteriorly to meet the oblique dorsal margin in a sharply rounded angle; posterior end of shell therefore produced and acuminate. Shells relatively swollen, posterior ridge very prominent; beaks slightly swollen, not elevated, strongly sculptured with V-shaped ridges, the posterior series the larger, not extending far beyond the beaks; beaks corroded and sculpture lost in adult shells.

Periostracum olive-brown to deep purple-brown, marked with fine growth lines and very prominent, dark rest marks. Nacre distinctly blue, slightly iridescent, stained coppery purple under the beaks. Shell substance relatively thick.

Hinge strong, unionid; cardinal teeth large, erect and grooved; lateral teeth relatively heavy, straight, short, and frequently grooved.

Anterior muscle scars deeply impressed, retractor separate as a pit under cardinal teeth; posterior scars very lightly impressed. Beak muscle scars deep and several in a row. Pallial line prominent only anteriorly.

Anatomy.—With the characters of the subgenus. Siphons prominent; anal with thick, muscular walls, branchial about 1¼ times size anal and bearing 3 rows of white papillae on internal face, innermost papillae larger and often dendritic. Siphonal area pigmented red-brown to black. Diaphragm long and perforate, larger perforation in females. Outer gills triangular and often fused together posteriorly; inner gills more elongate, attached to mantle anteriorly and dorsally. Palps small, subtriangular. Marsupium a well-marked pouch in inner third of inner gill of females. Outer gill in both sexes thin and not looped; interlamellar junctions few, weakly developed, and irregularly spaced; interfilamentar junctions thick-walled and regular. Inner gill of female in non-marsupial region as above. Marsupium with numerous, discontinuous, interlamellar junctions with very folded walls, fairly dense connective tissue, prominent muscle strands, and typically with a large sinus at each end. Chitinous supporting rods heavy and discontinuous (Plate 18, Fig. 3).

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
P. narracanensis								
Holotype	25	5	20%	15	60%	13	87%	7
Mean 4 paratypes	28	6	21%	16	57%	14	87%	9

*These paratypes, from Birregurra, are a mixed series, containing juvenile *Velesunio ambiguus* and *H. depressa*.

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
R. depressa sodalis								
Holotype, ex May's fig.	52	12	24%	28	54%	24	86%	?
Mean 8 specimens, Gippsland; NMV	25	6	24%	15	60%	13	87%	8
Mean 5 juveniles, Gippsland; NMV	17	4	23%	11	62%	9	82%	5
Mean 5 specimens, South Esk R., Tas.; QVML	35	6	18%	20	57%	16	80%	11
Mean 5 specimens, Liffey R., Tas.; ZDQ	56	14	25%	31	55%	26	84%	18

Material Examined

As above and specimens from VICTORIA: Mitchell R.; Narracan R.; Yarra R.; Winchelsea; Gembrook; Erskine R., Lorne. TASMANIA: Liffey R., Bishopsbourne; South Esk R., Ben Lomond.

Fig. 16.—Distribution of subfamily Hyridellinae (*continued*): 1, *Hyridella* (*H.*) *narracanensis*; 2, *H.* (*P.*) *glenelgensis*.

Range

Coastal streams of Victoria east of Yarra River, and Tamar River system, Tasmania (Fig. 16).

HYRIDELLA (HYRIDELLA) AUCKLANDICA (Gray)

Plate 12, Figs. 13–17

Unio aucklandicus Gray, 1843, p. 257.

Unio lutulentus Gould, 1851 (in part), p. 295; 1852 (in part), p. 428, pl. 37, fig. 542*c* (not figs. 542, 542*a*, and 542*b*.)

Diplodon lutulentus (Gould), Suter, 1913 (in part), p. 939, pl. 39, fig. 2.
Diplodon (*Hyridella*) *lutulentus* (Gould), Simpson, 1914 (in part), pp. 1301–2.
Hyridella aucklandicus aucklandicus (Gray), Dell, 1953, (in part), pp. 223–4, *only* pl. 17, figs. 5 and 6, pl. 19, figs. 2 and 3 (all of holotype).

Remarks

The present species has been misunderstood by previous authors, including Dell (1953). This has been so, because the type of *Unio aucklandicus* Gray had never been figured and because *Unio lutulentus* Gould was described from a series consisting of three species found in New Zealand. *Unio aucklandicus* Gray is a species of *Hyridella* occurring in both Islands, sympatrically with *Hyridella menziesi*, but far less commonly. It is quite distinct from *H. menziesi* and far less variable a species.

Dell (1953) examined photographs of the holotype of *U. aucklandicus* and associated it as a smooth subspecies of *Diplodon websteri* Simpson; the name *aucklandicus* had priority and became the nominate form. Dell mentioned that "no specimens have been seen with the sinuous ventral and rounded posterior margins of the type, but the type is evidently a much eroded shell".

Though Gray's description does not fully agree with the type, the type must be accepted. Dell's *Hyridella aucklandica aucklandica*, with the exception of the type, represents, in fact, a smooth subspecies of *Diplodon websteri* Simpson, which is regarded here as a species of the genus *Cucumerunio* Iredale. *Unio aucklandicus* Gray is distinct from either form in shell sculpture, shape, and hinge structure.

True *aucklandicus* Gray has long been known as *lutulentus* Gould. As outlined below (under *H. menziesi* (Gray)) the type series of *lutulentus* comprises three species. The lectotype, a form of *menziesi* with reduced winging, was called *aucklandicus* by Suter (1913). The usage of the two names, as examination of the types has revealed, was, in fact, reversed. Some paratypes of *lutulentus* are, however, true *aucklandicus* and *lutulentus* is listed here as a synonym, in part, of *aucklandicus*.

Types

Unio aucklandicus Gray: Holotype BM Reg. No. 1951-9-6-17. (The photograph shows that the "type" consists of two unmatched valves, both, apparently, of the same form.) Type locality: near Auckland, North Island; here restricted.*

Unio lutulentus Gould: Paratypes belonging to the present species are in USNM Reg. No. 87847. Type locality: New Zealand. Dell (1953) has suggested Bay of Islands as restricted type locality.

Description

Shell Morphology.—Shells elongate, of medium size, maximum length about 80 mm, MHI 45–50 per cent. Anterior portion of shell relatively short, BLI 15–20 per cent. Anterior margin rounded, ventral margin typically sinuate in the middle; dorsal margin posterior to beaks very slightly elevated, BHI about 88 per cent.,

*Gray gave two type localities, "Bay of Islands" and "Auckland in the Bay of Amabrusa". Dell (1953) thought Bay of Islands more likely as it agreed with the range of the form he called "*aucklandicus*" (= smooth subspecies of *Cucumerunio websteri*). Shells from Auckland closely resemble the holotype of *aucklandicus* and though Bay of Islands is possibly correct also, the type locality is restricted as above.

then dropping off evenly towards the ventral, rarely obliquely truncate; posterior margin evenly rounded. Shell moderately swollen, posterior ridge a little prominent, posterior slope somewhat compressed; beaks not swollen, low, sculptured with V-shaped ridges.

Periostracum dark brown to black, greenish in young specimens, often covered with a thick crust of iron carbonate, marked by fine growth lines. Nacre dull blue-grey, stained purple near beaks; shell substance fairly thick, particularly on the antero-ventral margin.

Hinge strong, unionid; cardinal teeth thickened, serrated, and grooved, anterior tooth of right valve reduced to a ridge; laterals long, gently curved.

Anterior muscle scars firmly impressed, anterior retractor and adductor almost fused; posterior scars and pallial line usually lightly impressed; beak muscle scars several, in a row.

Anatomy.—Gould (1852) figured a "paratype" of *Unio lutulentus* belonging to the present species; from the details visible, the anatomy appears to conform to that typical of the subgenus.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. aucklandicus Holotype, left valve ex photo.; BM	73	14	19%	33	45%	29	88%	?
U. aucklandicus Holotype, right valve ex photo.; BM	76	16	21%	38	50%	33	87%	?
U. lutulentus Mean 5 paratypes; MCZ	59	11	19%	28	48%	24	88%	15
Mean 4 specimens Pasadena, Auckland; MCZ	65	12	18%	34	52%	27	86%	19

Material Examined

As above and from Auckland (North Island) and Lake Coleridge, near Canterbury (South Island).

Range

Rare, from scattered localities in both islands of New Zealand.

Hyridella (Hyridella) misoolensis (Schepman)

Plate 13, Figs. 1–3

Unio misoolensis Schepman, 1897, p. 259, text fig. Drouet, 1897, pp. 125–6.
Virgus misoolensis (Schepman), Simpson, 1900, p. 852.
Virgus (*Leiovirgus*) *misoolensis* (Schepman), Haas, 1912, p. 133, pl. 13, fig. 3; 1924, p. 67. Simpson, 1914, p. 1153.
Virgus lorentzi Schepman, 1919, pp. 186–7, pl. 7, fig. 2.

Ctenodesma (*Nesonaia*) *misoolensis* (Schepman), Haas, 1923, p. 193.
Ctenodesma (*Nesonaia*) *lorentzi* (Schepman), Haas, 1923, p. 194.
Virgus (*Leiovirgus*) *lorentzi* (Schepman), Haas, 1924, pp. 67–8, pl. 2, fig. 9.
Leiovirgus guppyi misoolensis (Schepman), Riech, 1937, pp. 86–7.
Leiovirgus guppyi lorentzi (Schepman), Riech, 1937, pp. 86–7.
Leiovirgus misoolensis (Schepman), McMichael, 1956, pp. 42–4, pl. 2, figs. 6 and 7.
Leiovirgus lorentzi (Schepman), McMichael, 1956, p. 44.

Remarks

This, the type species of *Leiovirgus* Haas, has been known until now from very few specimens. Schepman, in the original description of the species. mentioned microscopic wrinkles of the epidermis extending down the posterior slope. This has led all subsequent workers to assume that the sculpture pattern was similar to that of the well-known species *guppyi* Smith, which has beak sculpture extending down the sides and slope of the shell as minute V-shaped wrinkles. Schepman's figure was not good enough to show the true condition of *misoolensis* sculpture. The relationship between this species and the New Guinea genus *Virgus*, first suggested by Simpson, has misled other workers, and McMichael (1956) has previously suggested that the relationship of *misoolensis*, *lorentzi*, and *guppyi* lies not with *Virgus* but with the Hyridellinae. Haas (1912) separated *misoolensis* from *Virgus*, s.s., as a subgenus, *Leiovirgus*, on the basis of the differences in shell sculpture. At the same time he created *Nesonaia* as a subgenus of *Ctenodesma* for the Solomon Islands species *guppyi*. Later, Haas (1923) recognized the similarity between *Nesonaia* and *Leiovirgus* and synonymized the two, using at first *Nesonaia* as a subgenus of *Ctenodesma*. In 1924, Haas realized that *Ctenodesma*, based on the Borneo species *borneensis* Issel, had little affinity with either form, so he transferred them to subgeneric relationship with *Virgus*. This time he used *Leiovirgus* on the grounds of page priority, but it was also of prior date as McMichael (1956) indicated. Haas commented on the conchological relationship between *guppyi* and the New Zealand species of *Hyridella*, but did not recognize that the true relationship lay with the Hyridellinae rather than with the cucumerunionine *Virgus*. Riech (1937) elevated *Leiovirgus* to full generic rank and McMichael (1956) accepted *Leiovirgus* as a full genus of the Hyridellinae, on the grounds of sculptural differences which were known for *guppyi* and had been indicated in *misoolensis* by Schepman. However, study of a large series of specimens of *misoolensis* from the Woru River at Seget, on the New Guinea mainland, close to Misool, reveals that the species does not possess extensive beak sculpture, but normal hyridelline V-shaped ridges only, not extending down onto the sides and slope of the shell. It is therefore necessary to transfer *misoolensis* to *Hyridella* s.s. and to place *Leiovirgus* in the synonymy of *Hyridella*. *Nesonaia* Haas may be resurrected for *guppyi* only, as it still differs from *Hyridella* s.s. in a number of characters. The large series of *H. misoolensis* from Seget also reveals that *Virgus lorentzi* Schepman must be considered only an ecophenotype of *misoolensis* as many Seget specimens approach *lorentzi* in every way. Further material from the Digoel River at Tanahmerah confirms the distribution of *misoolensis* right along the south coast of New Guinea as far as the Fly River, and the Lorentz River falls within the normal range of the species.

Types

Unio misoolensis Schepman: A series of four syntypes of this species is in the Rijksmuseum, Leiden. Dr. C. O. van Regteren Altena, Curator of Molluscs, informs us that the specimen figured by Schepman is among them, Cat. No. *Unio 7a*, and is the only adult shell in which the periostracum is preserved. It is therefore selected as lectotype and is figured here. Type locality: Misool, Dutch New Guinea.*

Virgus lorentzi Schepman: The unique holotype has not been located. Type locality: Alkmaar (Lorentz R.), Dutch New Guinea.

Description

Shell Morphology.—Shells medium-sized, maximum length about 70 mm, MHI 45–50 per cent. Shells elongate, more or less tapering posteriorly; anterior portion of shell short, BLI less than 20 per cent. Anterior margin evenly rounded, ventral margin long, slightly curved, almost straight or quite sinuate, dorsal margin sloping down behind the beaks or straight or slightly elevated, then sharply and acutely truncate; posterior end rather produced, rounded. Shells moderately swollen, posterior ridge rather pronounced with a shallow sulcation posterior to the ridge; posterior slope compressed. Beaks low, not swollen, sculptured with ridges, at first V-shaped, then separated below and tending to radiate from the beaks.

Periostracum dark brown, nacre bluish white, iridescent posteriorly, stained coppery yellow under the beaks. Shell surface with fine growth lines and a noticeable line above the posterior ridge, above which the growth lines appear closer together as they follow the acute angle of the posterior truncation. Shell substance relatively thin.

Hinge strong, with erect, serrated cardinal teeth, somewhat bifid in each valve in younger shells, becoming thickened and forming a crenated, irregular, heavy tooth in older shells; lateral teeth long, broad, and almost straight.

Anterior muscle scars strongly impressed, retractor separated from the adductor in a fairly deep pit. Posterior scars and pallial line lightly impressed.

Anatomy.—With the characters of the subgenus. Siphons of equal size and pigmented, branchial bearing 1–2 rows of small papillae internally. Labial palps small, subtriangular, each pair fused together posteriorly on their dorsal half. Gills very thin with weakly developed interlamellar junctions irregularly spaced and frequently discontinuous. Detailed structure of marsupium not known; male specimens only dissected here or Haas (1924). Foot small.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. misoolensis								
Holotype (ex Haas and Schepman)	65	11	18%	26	40%	24	92%	16

*During a recent visit to New Guinea, one of us (D.F.M.) attempted to confirm the locality of Misool for this species. Misool is a large island about 50 miles off the Dutch New Guinea coast. The island possesses several large rivers which could maintain a population of freshwater mussels, but, despite a fairly intensive search in one of these, none were found. Nevertheless, native inhabitants of the villages on Misool were quite definite in claims that the shells were to be found inland in the large rivers. Many shells were obtained from Seget, on the mainland, at a point opposite Misool, so it seems likely that this species does, in fact, come from the island.

Dimensions (continued)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
V. lorentzi								
Holotype (ex Schepman)	70	13	19%	31	44%	24	78%	17
Mean 10 specimens, Woru R., Seget; AM	56	11	20%	26	46%	23	88%	14
Kali Tap, Tanahmerah; AM	58	11	19%	22	38%	19	86%	12
Fly R.; AM	63	12	19%	26	41%	23	88%	17
Sorong; CMNH	43	7	16%	21	49%	18	86%	11

Material Examined

As above and specimens from Sorong; Woru R., near Seget; Kali Tap, near Tanahmerah (all Dutch New Guinea); Fly R. (Papua).

Range

Island of Misool and the south-western coast of New Guinea from the Vogelkop to the Fly River, Papua.

Subgenus ECHYRIDELLA, subgen. nov.

Type species: *Unio menziesi* Gray, 1843.

Remarks

The New Zealand species *Hyridella menziesi* (Gray) is widespread in both islands and is a remarkably variable form, particularly with regard to shape, shell thickness, and hinge development. Even with its variability it still conforms, in essential features, with the characteristics of the genus *Hyridella*. The material examined in the present work has shown a number of minor and mainly anatomical features which show little or no variability and which separate *H. menziesi* somewhat from the species included here in the subgenus *Hyridella*. As discussed below, it is probable that *H. menziesi* was introduced into New Zealand independently from and probably earlier than *H.* (*H.*) *aucklandica* and need not be regarded as a close relative of that species. We feel that subgeneric distinction for *H. menziesi* is warranted and the name *Echyridella* is proposed for it.

Diagnosis

Shell Characters.—Freshwater mussels of the genus *Hyridella* of medium size, maximum length about 100 mm. Shells elongate but outline very variable, MHI about 60 per cent., BHI about 75 per cent., BLI from 14 to 30 per cent. Hinge typically unionid, frequently reduced; sculpture confined to V-shaped ridges on the beaks; anterior muscle scars weakly to firmly impressed, adductor and retractor scars fused.

Anatomy.—With the general characters of the genus *Hyridella* but with thick, fleshy siphons and labial palps moderately large and of two parts, an anterior unridged portion and a subtriangular posterior region united posteriorly and dorsally for about half their length.

Glochidium.—Subtriangular, hooked, about 330μ in the hinge plane, 280μ deep.

Distribution

North and South Islands of New Zealand, except for the south-western part of the South Island.

Differential Diagnosis of Species

The subgenus is regarded here as monotypic.

Hyridella (Echyridella) menziesi (Gray)

Plate 14, Figs. 1–12

Unio menziesi Gray, 1843, p. 257. Hutton, 1882*a*, pp. 148–9, pl. 2.
Unio waikarense Colenso, 1845, p. 250 (footnote); 1882, p. 169. Hutton, 1882*b*, p. 170.
Unio lutulentus Gould, 1851 (in part), p. 295; 1852 (in part), p. 428; 1856, pl. 37, figs. 542, 542*a*, and 542*b* (but not fig. 542*c* = *H. aucklandica* (Gray)). Sowerby, 1868*a*, pl. 74, sp. and fig. 386.
Unio hochstetteri Dunker, 1862, p. 153. Sowerby, 1868*a*, pl. 86, sp. and fig. 463.
Unio menziesianus Gray, Reeve, 1865, pl. 29, sp. and fig. 152. (Error for *U. menziesi*.)
Unio aucklandicus Gray, Reeve, 1865, pl. 30, sp. and fig. 156. (Non *U. aucklandicus* Gray, 1843.)
Unio zelebori Dunker, 1866, p. 915. Frauenfeld, 1867, p. 15, pl. 2, fig. 28.
Unis (*sic*) *depauperata* Hutton, 1882*b*, p. 478; 1884, p. 216.
Unis (*sic*) *rugatus* Hutton, 1882*b*, p. 478; 1884, p. 216.
Diplodon (*Hyridella*) *menziesi menziesi* (Gray), Suter, 1905, pp. 234–6, text fig. 1. Simpson, 1914, pp. 1290–1.
Diplodon (*Hyridella*) *menziesi hochstetteri* (Dunker), Suter, 1905, pp. 237–8; 1913, p. 942, pl. 59, fig. 6. Simpson, 1914, p. 1292.
Diplodon (*Hyridella*) *menziesi lucasi* Suter, 1905, p. 239, text figs. 2 and 3; 1913, pp. 942–3, pl. 59, fig. 7. Simpson, 1914, pp. 1293–4.
Diplodon lessoni (Kuster) Suter, 1905, p. 240, text fig. 4. (Non *U. lessoni* Kuster, 1856.)
Diplodon menziesi acuta Suter, 1907, p. 239, pl. 22, figs. 11 and 12.
Diplodon (*Hyridella*) *lessoni* (Kuster), Suter, 1913, p. 938, pl. 59, figs. 1 and 1*a*. (Non *U. lessoni* Kuster, 1856.)
Diplodon (*Hyridella*) *lutulentus* (Gould), Suter, 1913 (in part), p. 939 (not pl. 59, fig. 2). Simpson, 1914 (in part), p. 1301.
Diplodon menziesi menziesi (Gray), Suter, 1913, p. 940, pl. 59, fig. 3.
Diplodon (*Hyridella*) *menziesi acutus* Suter, 1913, pp. 940–1, pl. 11, figs. 11 and 11*a*. Simpson, 1914, p. 1293.
Diplodon (*Hyridella*) *menziesi aucklandicus* (Gray), Suter, 1913, p. 941, pl. 59, fig. 4. Simpson, 1914, p. 1291. (Both non *U. aucklandicus* Gray, 1843.)
Diplodon (*Hyridella*) *menziesi depauperatus* (Hutton), Suter, 1913, pp. 941–2, pl. 59, fig. 5. Simpson, 1914, p. 1292.
Diplodon (*Hyridella*) *menziesi rugatus* (Hutton), Suter, 1913, p. 943, pl. 59, fig. 8.
Diplodon (*Hyridella*) *zelebori* (Dunker), Suter, 1913, p. 944, pl. 59, fig. 10. Simpson, 1914, p. 1295.
Diplodon (*Hyridella*) *menziesi rugulosum* Simpson, 1914, pp. 1291–2. (New name for *Unio rugatus* Hutton, 1882; non *U. rugatus* Menke, 1828, or *U. rugatus* Rossmassler, 1837.)
Diplodon (*Hyridella*) *waikarensis* (Colenso), Simpson, 1914, p. 1294.
Hyridella menziesi menziesi (Gray), Dell 1953, pp. 227–30, pl. 17, figs. 4 and 7, pl. 18, figs. 2–7, pl. 19, figs. 5 and 6.
Hyridella menziesi depauperata (Hutton), Dell, 1953, p. 231, pl. 17, figs. 9 and 10, pl. 18, figs. 1 and 8.

Remarks

The large number of synonyms listed above indicates that this is a particularly variable species. Dell (1953) has discussed, very adequately, many of the above synonyms, stressing that they are varieties and not distinct species or subspecies. It is not proposed, therefore, to duplicate his discussion here. In a few cases, however, additional information will be presented. Further, Dell admitted two subspecies, *Hyridella menziesi menziesi* (Gray) and *H. m. depauperata* (Hutton), which are not recognized here, and the reasons for this action will also be discussed.

Unio waikarense Colenso: Name applied to a large, thin, rounded form considered by Suter (1905) to be the same as *menziesi*. Simpson (1914) admitted the form as distinct, Colenso's (1845) description stating "posterior slope keeled, sharp", but Colenso probably implied that the shell was winged. There is no reason to assume that the form is anything but a slight variant of *menziesi*.

Unio lutulentus Gould: Dell (1953) synonymized this species with *H. aucklandica* (Gray) on the basis of a cotype in the Suter collection. Gould's description was based, however, on more than one species, an examination (by D.F.M.) of syntypes in the MCZ and USNM revealing the following:

(1) A low-winged form of *menziesi* with a thin shell and rather straight ventral margin.

(2) A thick-shelled form with no appreciable winging, a sinuate ventral margin, and an evenly rounded posterior margin. This form is the same as *U. aucklandicus* Gray and is listed under that species.

(3) A thin-shelled form with a strong hinge, nearly parallel dorsal and ventral margins, and a few nodules along the posterior ridge. This form is regarded as a subspecies of *Cucumerunio websteri* (Simpson), discussed below.

The shell figured by Gould (1852) in figs. 542, 542*a*, and 542*b* has been examined and belongs to the first series (low-winged *menziesi*) above and has been selected as lectotype by McMichael (1958). Sowerby's (1868) figure 386 is the same form. An earlier figure by Reeve (1865) under this name represents the third series mentioned above. *U. lutulentus* Gould is listed, therefore, as a synonym, in part, of *U. menziesi* Gray.

Unio aucklandicus Gray (Reeve 1865): Reeve's figure is of a low-winged specimen of *menziesi* which has since been referred to as *aucklandicus*. The type of *aucklandicus*, however, is a thick-shelled specimen with a sinuate ventral margin and distinct from Reeve's figure and from *menziesi*.

Unio zelebori Dunker: Dell (1953) has discussed the "*zelebori*" form and its occurrence over a fairly wide range. He also raises doubt concerning the real identity of Dunker's *zelebori*. For the present, without access to Dunker's types, we accept Dell's views and place *zelebori* as a synonym of *menziesi*.

Unio depauperata Hutton: A form of *menziesi* occurring in a few lakes and streams near Auckland and characterized by a weak shell and hinge. Another form, described as *Diplodon menziesi acuta* by Suter (1907), is very similar but with a stronger hinge and occurs in Lake Omapere, north of the range of *depauperata*.

Intermediate populations are typical *menziesi*. Dell has recognized the first two forms as one geographic subspecies, *Hyridella menziesi depauperata*, pointing out that *acuta* is difficult to place taxonomically. He states "if taxonomy is to express relationship, *acutus* must rank as a sub-subspecies of *depauperata*" and later "Later workers may find it necessary to re-establish *acutus* though the status of such a form must always remain a matter of opinion. It may well be that *acutus* is a subspecies in the making". There is no reason to assume that *acuta* is derived from *depauperata* and there is no biological basis for listing them as one geographic subspecies. Either both forms must be admitted or neither can be admitted. Dell's action in regarding them as the same subspecies seems to deny the geographical reality of the subspecies category. In the present account, perhaps conservatively, they are regarded as ecophenotypes only of *menziesi*.

Dell's discussion, with that given above, indicates that *H.* (*E.*) *menziesi* (Gray) is a very plastic species with a high degree of adaptability. It is possible that the species is a comparatively recent derivative from some Australian *Hyridella* stock and is now undergoing widespread adaptive radiation. Nearly every population reacts to its local environment to produce a different phenotype, and this variability is possibly accompanied by genetic differentiation. A classic example is seen in populations from two mountain lakes (Sarah and Grasmere), west of Christchurch, which are connected by a small stream, half a mile in length. The Lake Sarah population is fairly typical *menziesi* whereas the Grasmere population, living in deep mud, is the *hochstetteri* form. There is, however, no substantial evidence of geographic variation of the type which would allow the nomination of valid subspecies. The species is considered here as nomenclaturally monotypic.

Types

U. menziesi Gray: Holotype BM Reg. No. 42-5-17-170. Restricted type locality: Lake Taupo, North Island (selected by Dell (1953), p. 229.)

U. waikarense Colenso: Holotype unknown. A cotype in the Suter collection (Suter 1905, p. 236) now probably in DMW. Type locality: Lake Waikare, North Island.

U. lutulentus Gould: Lectotype USNM Reg. No. 5927. Paratypes USNM Reg. Nos. 85609, 87847, 17397, 129178, 17399, 17396; MCZ Reg. Nos. 88092, 155765. Type locality: Dell has suggested the area of Bay of Islands, here accepted.

U. hochstetteri Dunker: Holotype unknown, possibly in Vienna Museum. Type locality: "said to be in Lake Taupo and the Waikato River" (Dunker 1862).

U. zelebori Dunker: Holotype unknown, possibly in Vienna Museum. Type locality: New Zealand. Hochstetter, the collector, obtained material from a number of localities in both Islands, and no restricted type locality can be suggested.

U. depauperata Hutton: Dell selected a lectotype from two "syntypes" in the DMW, Reg. No. M.644, though Allan (1938, p. 182) stated that the type is in the Canterbury Museum, Christchurch, Reg. No. M. 670. Type locality: Lake Takapuna, near Auckland, North Island.

U. rugatus Hutton (subsequently *Diplodon menziesi rugulosus* Simpson): According to Allan (1938, p. 183,) the type is in the Canterbury Museum, Reg. No. M. 680. Type locality: Lake Pearson, South Island.

Diplodon menziesi lucasi Suter: Holotype DMW Suter Collection No. 5254. Type locality: Lake Manapouri, South Island.

"*Unio lessoni*": Shells identified by Dall and recorded by Suter under this name are in DMW and AM. They are from Lake Wakatipu, South Island.

Diplodon menziesi acuta Suter: Holotype DMW Suter Collection No. 5476. Paratypes DMW, AM Reg. No. C. 25498. Type locality: Lake Omapere, North Island.

Description

Shell Morphology.—Shells of moderate size, maximum length about 100 mm, usually not exceeding 70 mm, MHI about 60 per cent. Shells elongate to rounded, of very variable form; anterior portion of shell variously developed, BLI from 14 to 30 per cent. Anterior margin rounded, ventral margin usually quite curved, sometimes straight, in the *zelebori* form a little sinuate; dorsal margin usually quite elevated posterior to the beaks, BHI about 75 per cent. and the shell distinctly winged, but often only slightly so and in the *zelebori* form hardly at all (BHI 93 per cent.); antero-dorsal margin sometimes rounded, more usually obliquely truncate, in the *hochstetteri* form almost squarely so; postero-ventral margin rounded; posterior end somewhat deflected ventrally in the *zelebori* form. Shells usually not swollen, but variable; posterior ridge marked only in the *zelebori* form; beaks not swollen, and sculptured typically with small, V-shaped ridges, much reduced in the *zelebori* form.

Periostracum greenish to dark brown, marked by fine growth lines and often broken and scaly, particularly in the *hochstetteri* form. Nacre typically bluish, iridescent, variously stained. Shell substance of variable thickness, fragile and thin in *depauperata* forms, solid and thick in *zelebori* forms.

Hinge unionid, somewhat reduced; cardinal teeth thickened lamellae grooved and erect, sometimes peg-like (*zelebori*), sometimes reduced to thin lamellae or ridges (*depauperata*), the two teeth in the right valve frequently lying one behind, instead of diagonally above, the other; lateral teeth long, slightly curved, pustulose and serrated in the *zelebori* form, thin and delicate in the *depauperata* form.

Anterior muscle scars weakly to firmly impressed, anterior adductor and retractor fused, retractor forming a pit beneath the cardinal teeth only in the *zelebori* form; posterior scars and pallial line weakly impressed.

Anatomy.—Hutton (1882*a*) described the anatomy of this species and subsequent examination of the species confirms Hutton's observations in all respects but one, namely "the inner branchia is not united to the foot". In all specimens that we have examined, the inner lamella of the inner gill is attached to the foot anterior to its union with the corresponding lamella of the opposite inner gill. Our description is as follows: With the characters of the subgenus; siphons very prominent, thick, fleshy, well demarcated from mantle edge; mantle bridge between siphons well developed; siphonal area deeply pigmented brown to black; branchial siphon about twice size anal and bearing 2–3 rows of long, pale papillae. Gill diaphragm apparently imperforate. Outer gill subtriangular, attached to mantle along dorsal border; inner gill shallower, united to foot by its inner lamella. Palps moderately large, each of two parts, an anterior, unridged portion attached to mantle or foot, and a subtriangular posterior region, ridged on opposing faces, united posteriorly for about half their length, dorsally. Marsupium occupies middle third in inner gill of females. Outer gill of both sexes not looped, interlamellar junctions very few, irregular and discontinuous, interfilamentar junctions very long and thin-walled, discrete blood vessels almost absent, sinuses small. Inner gill of female in non-marsupial region as above, except for more extensive sinuses. Marsupium with

numerous, regular interlamellar junctions with thin, unfolded walls, diffuse connective tissue, very little musculature and continuous with extensive sinuses formed by interfilamentar junctions. Chitinous rods relatively large, at base of filaments.

Glochidium.—Percival (1931) has described the glochidium of "*Diplodon lutulentus*" (i.e. *H.* (*E.*) *menziesi*, as indicated previously) from shells collected in Lake Sarah. He gave the following dimensions: length 0·36 mm, depth from hinge to hook 0·28 mm. Measurements of glochidia collected recently show length 323μ and depth 277μ. The glochidia are subtriangular and hooked (see Percival 1931, figs. 1–3). Percival recorded natural infections of two juvenile fish, *Galaxias brevipennis* (lightly infected) and *Gobiomorphus gobioides*.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. menziesi Holotype, ex photo.; BM	54	9	17%	34	63%	25	74%	?
U. waikarense Holotype ex Colenso	89	?	?	57	64%	?	?	?
U. lutulentus Lectotype	57	11	19%	31	54%	25	80%	16
U. lutulentus Mean 5 paratypes; MCZ	55	11	20%	31	56%	25	80%	16
U. hochstetteri Type ex Dunker	60	?	?	39	65%	?	?	17
U. hochstetteri ex Sowerby fig.	52	10	19%	38	72%	27	71%	?
U. zelebori Holotype ex Dunker	50	?	?	26	52%	?	?	16
U. zelebori ex Frauenfeld fig.	57	15	26%	27	48%	25	93%	19
U. depauperata Lectotype ex Dell	58	8	14%	31	54%	21	68%	14
U. rugatus Holotype ex Hutton	52	?	?	34	66%	?	?	17
D. menziesi lucasi Type ex Suter	44	7	16%	24	55%	19	79%	?
D. menziesi acuta Type ex Suter	69	11	16%	38	55%	31	82%	?
"*D. lessoni*" ex Suter	50	9	18%	29	58%	21	72%	?
Mean 5 specimens, Te Papuni; DMW	90	18	20%	47	52%	37	79%	24
Mean 5 specimens, Rotorua; MCZ	59	10	17%	39	66%	30	77%	17
Mean 3 specimens, Lake Omapere; MCZ	77	13	17%	43	56%	34	79%	17

Material Examined

As indicated above and from: (*acuta* form) Lake Tangonge, Kaitaia; Lake Omapere (both North Island)—(*rugatus* form) Lake Waikare; Waikato R., Rangiriri (both North Island)—(*hochstetteri* form) Lake Taupo; Waikato R., below outlet of Lake Taupo, near Horotin; Lake

Rotorua; Lake Rotoiti; Ohinemutu, Lake Rotorua; Waitoa R., Morrinsville (all North Island); Lake Grasmere (South Island)—(*depauperata* form) Lake Takapuna; Lake Pupuke, Takapuna; Kaitaia R., near Auckland (all North Island)—(*zelebori* form) Albury Ck., Ashburton R.; Canterbury (all South Island) —(*zelebori/menziesi* forms) Porirua Stream, Porirua, near Wellington; Napier; Te Papuni (all North Island); Lake Alexandrina (South Island)—(*menziesi* form) Hokianga; Wellsford; Lake Tangonge, Kaitaia; Kaitaia R.; Parapara R., Mangonui; Western Springs, Auckland; Lake Horowhenua, Levin; Lake Wairarapa, Pinnoa; Waiuku, near Auckland; Kopuaranga R.; Lake Taupo; Lake Rotorua, Ohinemutu; Lake Rotoiti; Virginia Lake, Wanganui (all North Island); Nelson; Picton; Ashburton R.; Avon R.; Timaru; Christchurch; Lake Coleridge; Sawer's Ck., Greymouth; Lake Sarah (all South Island).

Range

Throughout the North and South Islands of New Zealand, except for the south-western part of the South Island.

Subgenus PROTOHYRIDELLA Cotton & Gabriel

Protohyridella Cotton & Gabriel, 1932, pp. 159–60. Type species by original designation: *Unio glenelgensis* Dennant, 1898.

Remarks

The genus was erected for a small unique mussel species from Victoria, separable from all other Australian species by its small size, strong shell sculpture and exceptionally strong hinge. Iredale (1934) commented that he had intended to separate *U. glenelgensis* subgenerically, but was anticipated by Cotton and Gabriel and accepted their procedure. While it is true that the strong shell sculpture is very characteristic, the resemblance to *Hyridella*, and especially to *H.* (*H.*) *narracanensis*, in all other characters suggests that only subgeneric distinction is warranted.

Diagnosis

Shell Characters.—Small, solid species of freshwater mussels of the genus *Hyridella*, amygdaloid in outline, winged posteriorly with a prominent posterior ridge, flattened posterior slope, and a produced, acuminate, posterior border. Beaks anterior, heavily sculptured, the sculpture extending to the shell, below the posterior ridge. Hinge very strong, with heavy grooved and denticulate cardinal and strong lateral teeth. Anterior muscle scars firmly impressed, adductor and retractor separate.

Anatomy.—Supra-anal opening absent. Siphons prominent, of equal size, anal brick red, branchial darker and bearing 3 rows of papillae internally. General anatomy similar to *Hyridella*, s.s.; palps relatively larger and extended posteriorly. Marsupium occupies middle third of inner gill of females.

Glochidium.—Unknown.

Distribution

Confined to the western coastal rivers of Victoria.

Differential Diagnosis of Species

The subgenus is monotypic.

Hyridella (Protohyridella) glenelgensis (Dennant)
Plate 13, Figs. 4–6

Unio glenelgensis Dennant, 1898, pp. 112–13, pl. iv.
Diplodon glenelgensis (Dennant), Simpson, 1914, p. 1290.
Protohyridella glenelgensis (Dennant), Cotton and Gabriel, 1932, p. 160, pl. xvi, fig. 9. Iredale, 1934, p. 74, pl. v, figs. 14*a* and 14*b*, pl. vi, fig. 14. Gabriel, 1939, p. 133, pl. iv, fig. 43. McMichael, 1952, p. 400, photograph p. 400. Kershaw, 1956, p. 54.

Remarks

This highly characteristic species has never been confused with any other Australian form. In general shape it resembles *Hyridella narracanensis*, but the latter never develops the heavy shell sculpture of the present species.

Types

Unio glenelgensis Dennant: Holotype NMV Reg. No. F. 627 (old number 58615). Paratype AM Reg. No. 6909. Type locality: Roseneath, Glenelg R., Vic.

Description

Shell Morphology.—Shells small, maximum length about 40 mm, MHI about 60 per cent. Shell outline amygdaloid, anterior portion of shell short, BLI about 20 per cent. Anterior margin rounded, ventral margin evenly curved, dorsal margin elevated posterior to beaks, then obliquely truncate, the shell appearing quite winged, BHI about 80 per cent.; posterior margin produced, acuminate. Shell slightly swollen, especially on young forms, posterior ridge very prominent, continuing to the posterior margin; posterior slope above ridge compressed, sometimes excavate. Beaks low, slightly swollen, strongly sculptured with V-shaped ridges. Shell surface, except for posterior slope, sculptured with a continuation of the beak sculpture, the ridges of the V's crossing below and continuing as wrinkles.

Periostracum olive-brown in young specimens, dark purple-brown in old. Nacre bluish, iridescent, stained pale brown under the beaks. Shell surface marked, apart from sculpture, with fine growth lines and regular, dark, rest marks. Shell substance heavy.

Hinge very strong; right cardinal tooth paired, the upper smaller, shorter, sharp, and lightly crenate and separated from the lower by a deep ridge, the lower tooth thick, heavy, erect, and denticulate on its inner face; left cardinal single, solid, peg-like, markedly denticulate. Lateral teeth long, slightly curved, heavy, slightly crenate.

Anterior muscle scars strongly impressed, retractor separate from adductor as a small deep pit beneath the cardinal tooth. Posterior scars lightly impressed; beak muscle scars 1 or 2. Pallial line lightly impressed even in old shells.

Anatomy.—Siphons prominent, anal somewhat conical, stained brick red, branchial almost same size, more deeply pigmented, and bearing internally 3 rows of papillae, the inner row of fewer, stouter papillae. Gill diaphragm minutely perforate. Outer gill triangular and free except at dorsal border of lamellae. Inner gill elongate, attached to foot dorsally and anteriorly. Palps relatively large, extended slightly posteriorly. Marsupium occupies middle third of inner gill of female. Outer gill of

both sexes not looped, interlamellar junctions few and irregular, interfilamentar junctions long and well vascularized. Non-marsupial region of inner gill of female as above. Marsupium with numerous interlamellar junctions of dense connective tissue, moderate muscular development and thick epithelium. Discrete blood vessels few. Chitinous rods large, at base of gill filaments.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. glenelgensis								
Holotype	38	8	21%	22	58%	18	81%	13
Paratype	41	10	24%	22	54%	18	81%	14
Mean 2 specimens, Port Fairy; AM	32	6	19%	19	59%	15	79%	11
Mean 5 specimens, Crawford R.; ZDQ	38	7	18%	22	58%	17	77%	13

Material Examined

As above and from Wannon Creek, near Hamilton; Glenelg R., Dartmoor.

Range

Coastal rivers of far western Victoria (Fig. 16).

Subgenus NESONAIA Haas

Nesonaia Haas, 1913, p. 132. Type species by original designation: *Unio guppyi* Smith, 1885.

Remarks

For many years the generic name *Nesonaia* has been regarded as a subjective synonym of *Leiovirgus* Haas, even as recently as McMichael (1956). However, the acquisition of a large series of specimens of *Unio misoolensis* Schepman, the type species of *Leiovirgus*, has convinced us that that species, together with its synonym *Virgus lorentzi* Schepman, cannot be separated generically from *Hyridella*, as the sculptural characters are not as described by previous authors. The Solomon Islands species *Unio guppyi* Smith, however, is very distinct in sculpture from *Hyridella*, s.s., and, together with its New Guinea mainland subspecies *aipianus* McMichael, is worthy of subgeneric distinction from *Hyridella*. It is therefore necessary to bring back *Nesonaia* Haas into use for *guppyi*, while *Leiovirgus* is placed in the synonymy of *Hyridella*.

Diagnosis

Shell Morphology.—Freshwater mussels of the genus *Hyridella* of small size, reaching about 80 mm in length. Shells elongate, MHI about 50 per cent., of unionine facies. Hinge very strong, unionid, with jagged, erect cardinals and long stout lateral teeth. Beaks sculptured with V-shaped ridges which break up over the disk of the shell as a series of small, irregularly V-shaped ridges which extend down the sides of the shell and down the posterior ridge and slope. Anterior muscle scars typically strongly impressed, with the adductor scar usually separate as a deep pit.

Anatomy (ex Haas 1924).—With the general characters of the genus. Anal siphon very long, pigmented; branchial siphon deeply pigmented and bearing several rows of short, sharp papillae. Mantle distal to pallial line pigmented light brown, proximal to pallial line pigmented dark brown posteriorly, otherwise flecked with brown pigment. Labial palps small, somewhat sickle-shaped, each pair fused posteriorly on their dorsal half. Outer gill of both sexes thin and with weakly and irregularly developed interlamellar junctions. Inner gill of female similar in non-marsupial region; marsupium small, occupying anterior third of inner gill and possessing numerous, closely packed interlamellar junctions. Histological details unknown.

Glochidium.—Unknown.

Distribution

The Solomon Islands and eastern New Guinea.

Differential Diagnosis of Species

The subgenus is monotypic, but two subspecies of *H.* (*N.*) *guppyi* are recognized. *H.* (*N.*) *guppyi guppyi* from the Solomon Islands may be separated from the mainland race *H.* (*N.*) *guppyi aipiana* by its smaller BLI which is 17–18 per cent. in *guppyi guppyi* and 23–26 per cent. in *guppyi aipiana*. *H.* (*N.*) *guppyi guppyi* is also relatively more winged posteriorly than *guppyi aipiana*.

Relationships

The subgenus is closely related to *Hyridella*, s.s., from which it differs only in the greater development of sculpture and the more unionid hinge. Some Queensland populations of *Hyridella* show a tendency to develop extended beak sculpture, though this never quite reaches the development found in *H.* (*N.*) *guppyi*. *Nesonaia* is almost certainly a derivative of *Hyridella*, probably through isolation in the Solomon Islands region. The mainland race may have been established through recolonization of the New Guinea mainland from the Solomon Islands.

Hyridella (Nesonaia) guppyi guppyi (Smith)

Plate 13, Figs. 7–10

Unio guppyi Smith, 1885, p. 608, pl. 37, figs. 8, 8*a*, and 8*b*.
Ctenodesma guppyi (Smith), Simpson, 1900, p. 853.
Ctenodesma (*Nesonaia*) *guppyi* (Smith), Haas, 1913, p. 137, pl. 13, figs. 6 and 7.
Cristadens guppyi (Smith), Simpson, 1914, p. 1156.
Virgus (*Leiovirgus*) *guppyi* (Smith), Haas, 1924, p. 69; 1930, pp. 271–4.
Leiovirgus guppyi guppyi (Smith), Riech, 1937, pp. 86–7. McMichael, 1956, pp. 45–6.

Remarks

This species is apparently quite common on most of the islands of the Solomon Group and is possibly the only known freshwater mussel species to occur on a group of islands of this type, distant from large land masses.

Simpson (1900) placed the species in *Ctenodesma* (a Borneo genus) but Haas (1913) separated it subgenerically. Simpson's later usage of *Cristadens* was due to the supposed preoccupation of *Ctenodesma*, but even in replacing the name (which

was unnecessary) he overlooked *Nesonaia* as a substitute. Later Haas (1924) concluded that *guppyi* did not belong with *Ctenodesma*, but was more closely related to the New Guinea species listed as *Virgus* (*Leiovirgus*) *misoolensis* (Schepman) and *V.* (*L.*) *lorentzi* Schepman. In a later paper, Haas (1930) gave anatomical data to support the relationship between *misoolensis*, *lorentzi*, and *guppyi* and so the relationship between the three species became accepted.

Riech (1937) treated the three forms as a *Rassenkreis* on the grounds of the more or less linear distribution of the three forms and because of a supposed progressive increase in the relative height of the shell from *misoolensis* in the north-west to *guppyi* in the east. Riech also gave full generic rank to *Leiovirgus*. It has now been shown that *misoolensis* is distributed right along the southern coast of New Guinea as far as the Fly River, with *lorentzi* as an ecophenotype only, and furthermore, *guppyi* is subgenerically separable from that species. McMichael (1956) accepted the group *Leiovirgus* for all three forms, but allowed *guppyi* full species rank, and named a new subspecies from the New Guinea mainland. At present *guppyi* is not recorded from the islands between the Solomon Group and New Guinea.

Types

U. guppyi Smith: Holotype BM Reg. No. 1885-11-3-461. Paratypes BM Reg. No. 1885-11-3-462. Type locality: Shortland Island, Solomon Group.

Description

Shell Morphology.—Shells medium-sized, maximum length about 80 mm, MHI about 50 per cent. Shells elongate oval, anterior portion of shell short, BLI less than 20 per cent. Anterior margin rounded, ventral margin rather straight, dorsal margin slightly elevated posterior to the beaks, then obliquely truncate, the shell appearing a little winged, BHI about 75–80 per cent.; posterior margin evenly rounded. Shells compressed, posterior ridge moderately swollen, the shells sometimes with a shallow sulcation anterior to the ridge; posterior slope compressed. Beaks low, only slightly swollen, sculptured with weak V-shaped ridges which break up below to give numerous, fine V-shaped wrinkles on the sides of the shell, and irregular ridges running up the posterior slope.

Periostracum olive-brown to dark brown; nacre bluish white, becoming iridescent posteriorly and stained copper to purple under the beaks. Shell surface with sculpture extending down from the beaks, otherwise marked with fine growth lines and often marked by the egg cases of the freshwater gastropod *Neritina* on the posterior portion of the periostracum. Shell substance moderately thick.

Hinge very strong in adult shells; the cardinals in both valves split up into a series of jagged and grooved teeth, but sometimes persisting as thick, serrated ridges or split longitudinally into two or more subsidiary teeth; lateral teeth long, fairly straight, strong lamellae.

Anterior muscle scars typically strongly impressed, retractor separate from adductor as a small, deep pit beneath the cardinal teeth. Posterior scars very lightly impressed; beak muscle scars variable, sometimes in a line, sometimes irregularly scattered in the beak cavity. Pallial line not prominent.

Anatomy.—With the characters of the subgenus.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	76	12	16%	36	47%	27	75%	20
Mean 2 paratypes	73	10	14%	34	47%	25	74%	19
Mean 5 specimens, Aola, Guadalcanal; MCZ	64	12	19%	32	50%	24	75%	16
Mean 2 specimens, Ugi I.; AM	60	11	18%	30	50%	24	80%	16
Mean 2 specimens, Fulakora, Santa Isabel; MCZ	39	8	21%	20	52%	16	80%	10

Material Examined

As above and from Marovovo (Guadalcanal); Cavaga Ck. (Guadalcanal); Shortland Island; Fui (= Fiu ?) (Malaita).

Range

From streams in the following islands of the Solomon Group: Guadalcanal, Shortland Island, Bougainville, Malaita, San Cristoval, Santa Isabel, and Ugi Island. It is not so far recorded from two of the larger islands, Choiseul and New Georgia.

Hyridella (Nesonaia) guppyi aipiana (McMichael)

Plate 13, Fig. 11

Leiovirgus guppyi aipianus McMichael, 1956, pp. 44–6, pl. 2, figs. 1 and 2.

Remarks

This mainland race is so far known only from the types. The species was sought on the north Papuan coast around Buna, but apparently does not live there. It may occur in streams along the coast of Papua, south-east of the St. Joseph's River, though it has not been found in streams near Port Moresby.

Types

Holotype QM Reg. No. Mo. 2798. Paratype AM Reg. No. C. 62203. Type locality: Aipiana, St. Joseph's R. (= Angabunga R.), Papua, New Guinea.

Description

Shell Morphology.—Shells small, maximum length (so far known) 44 mm, MHI 50 per cent. Shells elongate oval, anterior portion of shell moderately long, BLI about 25 per cent. Anterior margin rounded, ventral margin slightly curved, dorsal margin straight, not elevated posterior to the beaks, then obliquely truncate, the shell not noticeably winged, BHI 90–95 per cent.; posterior margin fairly evenly rounded. Shells compressed, posterior ridge not marked. Beaks low, sculpture developed as in the nominate subspecies.

Periostracum olive-brown, nacre bluish white, slightly iridescent, stained yellow to copper colour under the beaks. Shell surface marked with beak sculpture extending down the sides of the shell, and with well-marked growth lines. Shell substance rather thin.

Hinge strong; right cardinal teeth paired, the upper smaller, both grooved (both types are juveniles; the hinge teeth resemble those of *H.* (*N.*) *guppyi guppyi* of similar size); lateral teeth long, slightly curved, broad lamellae.

Anterior muscle scars rather weak, posterior scars and pallial line almost invisible.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	44	10	23%	22	50%	20	91%	10
Paratype	43	11	26%	22	52%	21	96%	10

Material Examined

Types only.

Range

Known only from the type locality.

Subfamily **CUCUMERUNIONINAE** Iredale

Subfam. Cucumerunionae (*sic*) (= Cucumerunioninae) Iredale, 1934, pp. 58 and 77.

Remarks

The subfamily was erected for one Australian mussel species morphologically distinct from all other Australian forms. This species, *Cucumerunio novaehollandiae* (Gray) is characterized by its size and strong shell sculpture. Iredale made no attempt to define the subfamily other than to comment "Beaks plicate [i.e. sculptured], shell large". Such a diagnosis served, at the time, to separate the group from the other Australian subfamily with sculptured beaks (Propehyridellinae = Hyridellinae). Additional species included in the subfamily Cucumerunioninae render Iredale's diagnosis inadequate and the taxon must be redefined.

Modell (1942) placed the subfamily in the family Margaritiferidae Ortmann, and admitted two genera, *Cucumerunio* Iredale and *Virgus* Simpson, in it. His inclusion of New Zealand along with New Guinea and Australia in the distribution of the subfamily indicates his inclusion of the New Zealand species *Cucumerunio websteri* (Simpson).

In the present work, Modell's arrangement is followed, except that the subfamily is referred to the family Mutelidae Gray, on anatomical grounds. The similarity of *Virgus* and *Cucumerunio* is unmistakable and the relationship between them and the subfamily Hyridellinae is close.

Diagnosis

Freshwater mussels of the family Mutelidae with sculptured beaks and shells, elongate form, and of variable size. Shell sculpture typically of nodules or ridges on the posterior ridge and spreading dorsally and ventrally from it. Hinge strong, unionid; cardinal teeth very erect, grooved, serrated, and frequently denticulate. Anterior retractor muscle scar tending to separate from adductor as a pit under the cardinal teeth. Supra-anal opening absent; siphons large and prominent, of equal size; mantle bridge between siphons thick, branchial siphon papillate and open below. Marsupium occupies middle four-fifths of inner gill of females and possesses numerous, incomplete septa with heavy musculature. Glochidium unknown.

Present Distribution

Eastern Australia, North Island of New Zealand, and southern New Guinea.

Fossil Record

No fossils known.

Genus CUCUMERUNIO Iredale

Cucumerunio Iredale, 1934, p. 75. Type species by original designation: *Unio novaehollandiae* Gray, 1834.

Cucumaria Conrad, 1853, p. 269. Type species by monotypy: *Unio cucumoides* Lea, 1840 (= *Unio novaehollandiae* Gray, 1934).

NOT *Cucumaria* Blainville, 1830 (Echinodermata) OR Lesson, 1831 (Echinodermata).

Cucumeria Simpson, 1900, p. 893. (Error for *Cucumaria* Conrad, 1853).

Remarks

Conrad's name for this group, though doubly preoccupied, stood for many years until Iredale (1934) provided a substitute name for it. Simpson's name *Cucumeria* was unquestionably a typographical error, for Simpson himself later (1914) corrected it to *Cucumaria*. The name *Cucumeria* is therefore an Erroneous Subsequent Spelling which has no separate status in nomenclature (see Copenhagen Decisions on Zoological Nomenclature, 1953, Nos. 71, 72, 73, pp. 43–5).

When Iredale renamed the genus it was left monotypic, although Simpson (1914) had used *Cucumaria* Conrad as a section of the subgenus *Hyridella* and included three species, *U. novaehollandiae* Gray, *U. shuttleworthi* Lea (a misidentification), and *Diplodon websteri* Simpson. The systematic position of *websteri*, a New Zealand species, has been much debated. Suter (1905) placed little value on the shell sculpture and associated it with *Hyridella menziesi* (Gray). Dell (1953) recognized the specific distinctness of the form but left it in the genus *Hyridella* with the remainder of the New Zealand species. The similarity between *Cucumerunio novaehollandiae* and *websteri* is unmistakable, even though some populations of *websteri* lack the characteristic shell sculpture. The diagnosis of Iredale's genus is therefore broadened to include it.

Diagnosis

Shell Characters.—Freshwater mussels of the subfamily Cucumerunioninae of medium to large size, reaching 200 mm in length. Shells elongate, MHI less than 50 per cent.; beaks anterior, BLI about 20 per cent.; maximum height of shell close

to position of beaks, BHI usually more than 90 per cent. Beaks sculptured with V-shaped ridges, the sculpture continuing on to the posterior portion of the shell as lachrymose nodules, sometimes fused as ridges, sometimes spreading to the anterior portion of the shell, sometimes absent. Hinge well developed; lateral teeth long, heavy; cardinal teeth erect, serrated, denticulate, sometimes reduced. Anterior muscle scars firmly impressed, anterior retractor and adductor fused; pallial line well marked.

Anatomy.—Supra-anal opening absent; siphons large and prominent, mantle bridge thick; siphons of equal size, branchial papillate. Gill diaphragm short and minutely perforate. Palps large, semilunar. Outer lamellae of outer gills completely fused to mantle, inner lamellae of inner gills completely fused to visceral mass dorsally and anteriorly. Marsupium occupies middle four-fifths of inner gill of females and possesses numerous interrupted interlamellar junctions with thick, folded walls, diffuse connective tissue and heavy musculature and typically with a blood sinus at each end (Plate 18, Figs. 6 and 7).

Glochidium.—Unknown.

Distribution

Central part of east coast of Australia and North Island of New Zealand.

Differential Diagnosis of Species

C. novaehollandiae (Gray) is an Australian species, large, elongate, frequently linguiform, with a regularly developed shell sculpture confined to the posterior portion of the shell, with a BHI of about 80 per cent. and MHI of 40 per cent. *C. websteri* (Simpson), from New Zealand, is smaller, with shell sculpture less regularly developed, MHI of about 50 per cent. and BHI of more than 90 per cent. The two subspecies can be distinguished thus: *C. websteri websteri* is small and extensively sculptured while *C. websteri delli* is larger, relatively more elongate, and lacking in shell sculpture.

Relationships

The genus is unique in its shell sculpture and characteristic hinge. It appears to be closely related to *Virgus* Simpson and more distantly to members of the subfamily Hyridellinae. No fossil species are known.

Cucumerunio novaehollandiae (Gray)

Plate 15, Figs. 1–4; Plate 18, Figs. 6 and 7

Unio novaehollandiae Gray, 1834, p. 57. Hanley, 1843, p. 182. Smith, 1881, p. 312.

?*Naia elongata* Swainson, 1840, p. 285. (Nomen nudum.)

Unio cucumoides Lea, 1840, p. 285; 1842, p. 192, pl. 7, fig. 2. Chenu, 1847, pl. 27, figs. 3, 3*a*, and 3*b*. Conrad, 1853, p. 269. Hanley, 1856, p. 382, pl. 24, fig. 4. Kuster, 1861, p. 219, pl. 74, fig. 1. Reeve, 1865, pl. xx, sp. and fig. 89.

Unio cumingianus Dunker, 1852, p. 53.

Unio cumingii Dunker, Lea, 1870, p. 31. (Name in error.)

Diplodon (*Hyridella*) *novaehollandiae* (Gray), Simpson, 1914, p. 1304.

Diplodon (*Hyridella*) *shuttleworthii* (Lea), Simpson, 1914, p. 1306. (Non *Unio shuttleworthi* Lea, 1856.)

Cucumeria novaehollandiae (Gray), Cotton and Gabriel, 1932, p. 160, pl. xvi, fig. 7.

Cucumerunio novaehollandiae (Gray), Iredale, 1934, p. 75, pl. v, fig. 15, pl. vi, fig. 15. McMichael, 1952, p. 400, photograph p. 398.

Remarks

Though this species is the most easily recognizable of all the Australasian mussels, it was given three names within 20 years, viz. *novaehollandiae* Gray, *cucumoides* Lea, and *cumingianus* Dunker. The type of *novaehollandiae* was never figured, but Smith (1881) had access to it at the British Museum and correctly synonymized *cucumoides* with it. The exact identity of *cumingianus* is somewhat doubtful as it has never been figured and Dunker's types are not apparently available. Dunker's description, though brief, has been adequate for most subsequent workers to synonymize his species with *novaehollandiae*.

Simpson's puzzling error in identification of *Unio shuttleworthi* Lea has been discussed by Iredale (1934, pp. 63 and 76). Frierson (1908) reiterated Simpson's error.

Types

Unio novaehollandiae Gray: Syntypes BM Reg. No. 80-4-10-6, consist of two left valves. Type locality: Macquarrie (*sic*) R. The Macquarie River is, however, part of the Murray–Darling system and the species does not occur there. The correct locality may be Port Macquarie, on the north coast of New South Wales, at the mouth of the Hastings River, which is within the range of the species.

Unio cucumoides Lea: Holotype AMNH Reg. No. 30897. Type locality: Hunter River, N.S.W.

Unio cumingianus Dunker: Holotype unknown. Type locality: "New Holland". Lea's (1870) use of the name "*U. cumingii* Dunker", quoting Dunker's original reference incorrectly and giving Richmond River as locality cannot be considered seriously.

Description

Shell Morphology.—Shells elongate, reaching a maximum length of about 200 mm, MHI about 40 per cent. Shell outline elongate oval in juveniles, elongate oblong in medium-sized specimens, to distinctly linguiform in old specimens. Anterior portion of shell short, BLI about 20 per cent. Dorsal margin usually slightly excavate anterior to beaks, rising slightly posterior to beaks, usually somewhat obliquely truncate posteriorly in young shells but less so or gently rounded in old; ventral margin evenly rounded in young shells, straight in medium-sized shells and sinuate in old, the posterior region of the margin sometimes dipping in a pronounced fashion; posterior margin slightly produced, square, or evenly rounded; anterior margin rounded, more so dorsally. Shells not swollen, anterior part compressed, posterior ridge quite prominent, posterior slope compressed, sometimes excavate. Beaks not swollen, very low in large shells, sculptured with V-shaped ridges, usually corroded.

Periostracum olive-green in juveniles, brown to brilliant black in adults; growth lines prominent, rest marks sometimes deeply marked. Nacre whitish, markedly iridescent anteriorly, marked with copper-coloured blotches. Shell substance thick, particularly antero-ventrally. Shell surface almost unsculptured in juveniles, heavily sculptured in mature shells, the sculpture in the form of raised bars and ridges covering the entire posterior surface, diminishing and finally disappearing anteriorly. In uneroded shells, the sculpture pattern shows as a series of ridges running down the posterior ridge to its extremity and spreading dorsally and ventrally, particularly to the posterior slope.

Hinge strong, horny portion standing well above the dorsal margin of the shell. Cardinal teeth heavy and erect, usually grooved and serrated, sometimes flattened as a series of denticles; in old shells usually reduced to smooth, large nodules. Lateral teeth long, straight, heavy, and blade-like, double in left valve, single in right.

Anterior muscle scars deeply impressed, particularly in old shells, adductor and retractor almost separate, retractor forming a large, deep pit beneath the cardinal teeth. Posterior scars lightly but obviously impressed. Beak muscle scars numerous, in a row under the beaks.

Pallial line very deeply impressed as a pitted groove in old shells posteriorly, less obvious anteriorly.

Anatomy.—With the characters of the genus. Siphons large and prominent, mantle bridge prominent; anal siphon pigmented deep brown with black blotches, branchial of same size, much darker and bearing 3 rows of papillae, the inner row fewer and larger. Gill diaphragm short and minutely perforate. Outer gill triangular and free except at dorsal border; inner gill elongate and free except on dorsal and anterior borders. Palps large, semilunar, finely ridged on opposing faces. Marsupium occupies middle four-fifths of inner gill of females. Outer gills in both sexes irregularly looped with few, irregularly spaced interlamellar junctions with well-developed walls and traces of musculature; interfilamentar junctions on outer lamella short, thick-walled, and enclosing a discrete blood vessel; on inner lamella long, thin-walled, enclosing a spacious blood sinus. Inner gill of female as above in non-marsupial region, but with more interlamellar junctions. Marsupial region with many interlamellar junctions with thick, folded walls, heavy musculature, and diffuse connective tissue, typically with a blood sinus at each end; mostly forming short, discontinuous septa with blood sinuses. Ventral margin of inner gill grooved. Chitinous supporting rods very heavy, at base of filaments (Plate 18, Figs. 6 and 7).

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. novaehollandiae								
Syntypes, Valve 1	135	25	18%	48	36%	40	83%	?
Valve 2	137	25	18%	50	36%	40	80%	?
U. cucumoides								
Holotype	141	22	16%	53	38%	44	83%	35
Mean 10 specimens, juveniles, Brisbane R.; ZDQ	69	13	19%	29	42%	23	79%	16
Mean 10 specimens, North Pine R., near Brisbane; ZDQ	155	34	22%	63	41%	50	79%	41

Material Examined

As above and from NEW SOUTH WALES: Hunter R.; Manning R., Mt. George; Charity Ck., near Taree; Hastings R., Port Macquarie; Richmond R., Booyong, Casino; Barrington R.; Tweed R., Byangum, Crystal Ck., near Murwillumbah. QUEENSLAND: Brisbane R., Wyvenhoe; Stanley R.; North Pine R., near Petrie; Upper Nerang R.; Burnett R.

Range

Coastal rivers of eastern Australia from Hunter River, New South Wales, north to Burnett River, Queensland.

Cucumerunio websteri websteri (Simpson)

Plate 15, Figs. 5–9

Unio lutulentus Gould, Reeve, 1865, pl. 25, sp. and fig. 122. (Non *U. lutulentus* Gould, 1851.)
Diplodon websteri Simpson, 1902, p. 30. Suter, 1905, p. 236; 1906, p. 270. Dall, 1909, p. 181, pl. xxx, figs. 1 and 2.
Unio (*Diplodon*) *websteri* Simpson, Webster, 1906, p. 311, pl. 39, figs. 5, 5*a*, and 5*b*.
Diplodon (*Hyridella*) *menziesi websteri* Simpson, Suter, 1913, pp. 943–4, atlas pl. 59, fig. 9.
Diplodon menziesi websteri Simpson, Powell, 1937, p. 25.
Hyridella aucklandica websteri (Simpson), Dell, 1953, pp. 225–6, pl. 17, figs. 1 and 3, pl. 19, fig. 1.

Remarks

Despite Simpson's description of the present species, his placing it, with *Unio novaehollandiae* Gray, in his "Section *Cucumaria*" and the good illustrations by both Webster (1906) and Dall (1909) which clearly illustrate the shell sculpture pattern and hinge structure, the status of the species has been a matter of much debate. Dell (1953) has discussed the species and reached a fairly satisfactory concept of it, but has used the name *aucklandicus* Gray for it. McMichael (1958) has shown that *aucklandicus* Gray belongs with *Hyridella*, as discussed previously under that heading. The present species is, as Simpson suggested, obviously related to *Cucumerunio novaehollandiae* (Gray). Dell did not regard shell sculpture as a taxonomic feature permitting generic distinction and a study of New Zealand forms alone would certainly lead to that conclusion.

In Australia, *Cucumerunio novaehollandiae* retains its sculpture throughout its range; *C. websteri* tends to lose its sculpture in the northern half of its range. The sculptureless form is regarded here as subspecifically different, but its other characters indicate quite clearly its relationship with the present species and with *Cucumerunio*.

Reeve's (1865) figure, labelled "*Unio lutulentus* Gould", represents the first published figure of the present species; though the sculpture is merely indicated, the characteristic form is shown.

Powell (1937) gave information on the type locality of *websteri* and stated that the species had not been found since its original discovery. Dell (1953) has figured a specimen from Lake Kaitoke, Wanganui, and several subfossil occurrences are known, indication that the species is not merely a pathological freak.

Types

No holotype designated, dimensions of two specimens given. Dall (1909) figured the larger specimen, USNM Reg. No. 162342, here selected as lectotype. Paratypes, USNM 162342*a*, MZUM Reg. No. 18617, CNHM Reg. No. 21736. Additional paratypes in DMW and AM. Type locality: Waiuku, North Island, N.Z.

Description

Shell Morphology.—Shells elongate, maximum length about 70 mm, MHI about 50 per cent. Anterior portion of shell relatively short, BLI about 20 per cent.

Anterior margin truncated in front of beaks then rounded; ventral margin straight; dorsal margin posterior to beaks straight or slightly elevated, subparallel to ventral margin, then obliquely truncate; posterior margin fairly straight, meeting ventral margin in a bluntly rounded angle. Shells thin, compressed; beaks low, not swollen, sculptured with V-shaped ridges. Shell surface marked with lachrymose nodules loosely patterned in a row down posterior ridge and spreading dorsally and ventrally from it; nodules on anterior part of shell also, radiating from beaks.

Periostracum olive-green to brown, often coated with blackish stains; growth lines fine, rest marks frequently very prominent. Nacre bluish white with purplish or yellow spots.

Hinge complex, strong; cardinal tooth double in right valve, anterior tooth reduced, posterior tooth grooved and serrated; single strong, crenate cardinal in left valve, sometimes with a posterior accessory tooth; cardinals sometimes reduced in older shells; lateral teeth strong, straight lamellae.

Anterior muscle scars strongly impressed, retractor and adductor scars fused, protractor scar almost separate; posterior scars and pallial line faint.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Lectotype	66	12	18%	33	50%	29	88%	15
Paratypes USNM								
Specimen 1	69	13	19%	34	49%	32	94%	16
Specimen 2	61	12	20%	30	49%	28	93%	14
Specimen 3	59	14	24%	31	52%	29	93%	18
Specimen 4	26	6	23%	14	54%	13	93%	6
Paratypes DMW ex Dell								
Specimen 1	60	14	23%	32	53%	27	84%	16
Specimen 2	69	18	26%	33	48%	?	?	17
Paratypes MZUM								
Specimen 1	82	14	17%	39	48%	33	85%	20
Specimen 2	63	14	22%	31	49%	29	93%	15
Specimen 3	48	10	21%	23	48%	22	96%	10
Paratype CNHM	64	13	20%	29	46%	27	93%	14

Material Examined

Waiuku, North Island, N.Z.

Range

Dell (1953) records the range as "scattered occurrences south of Auckland, as far as Foxton".

Cucumerunio websteri delli, subsp. nov.

Plate 16, Figs. 1–5

Hyridella aucklandica aucklandica Gray, Dell, 1953 (in part), pp. 224–5, pl. 17, figs. 2 and 8, pl. 19, figs. 4 and 8. (Non *Unio aucklandicus* Gray 1843.)

Remarks

As mentioned previously, Dell (1953) recognized that two geographic races could be differentiated in the present species. He used the name *aucklandicus* Gray for the smooth subspecies, basing his opinion on a photograph of the holotype of *Unio aucklandicus* Gray from the British Museum. He stated (p. 224) that "no specimens of this form [i.e. *C. websteri delli*] have been seen with the sinuate ventral and rounded posterior margins of the type, but the type is evidently a much eroded shell and the sinuous ventral margin is a common response by mussels living in stony streams". While we agree that sinuation of the ventral margin is commonly an ecophenotypical character developed by stream populations, we believe that the holotype of *U. aucklandicus* is quite distinct from the present form. It represents a species of *Hyridella*, subgenus *Hyridella*, occurring near Auckland and has been described previously as *Hyridella* (*H.*) *aucklandica*. As a consequence, only the sculptured subspecies, *websteri* Simpson, has a name. The reference above only partly applies to the present form since Dell included the holotype of *U. aucklandicus* in his concept of the species.

The sculptured race becomes the nominate subspecies, while the sculptureless northern form is named *Cucumerunio websteri delli*, subsp. nov., in honour of Dr. R. K. Dell, Conchologist, Dominion Museum, Wellington, N.Z.

Types

Holotype AM Reg. No. 61929. Paratypes MCZ Reg. No. 190253. Type locality: Omaha R., near Leigh, North Island, N.Z. Other paratypes MCZ Reg. No. 82226, from Henderson, near Auckland. The description below is based partly on two specimens figured by Dell (1953), one from Kaikohe (pl. 17, fig. 2) and one from Kaeo (pl. 17, fig. 8, pl. 19, fig. 8), and studied by one of us. These are therefore paratypes.

Description

Shell Morphology.—Shells elongate, maximum length about 90 mm, MHI about 47 per cent. Anterior portion of shell relatively short, BLI about 20 per cent. Anterior margin somewhat truncated, rounded below; ventral margin straight or very slightly sinuate; dorsal margin posterior to beaks not elevated but falling off gently towards ventral margin; obliquely truncate posteriorly; posterior margin meets ventral margin in a bluntly rounded angle. Shells not swollen, sides flattened, sometimes slightly sulcate ventrally; beaks not swollen, low, sculptured with V-shaped ridges; posterior ridge marked off from posterior slope by a faint groove.

Periostracum olive-green to dark brown, thick, marked by fine growth lines and regularly spaced rest marks which cause undulations on the shell surface. Nacre bluish white, stained with purple and coppery spots. Shell substance solid, especially anteriorly below pallial line.

Hinge strong; lower cardinal tooth of right valve long, broad, erect, grooved, serrated, and denticulate. Lateral teeth long, straight lamellae.

Anterior muscle scars firmly impressed, anterior retractor deep but fused to adductor scar; posterior scars light; beak muscle scars 4 or 5 in a row. Pallial line well marked.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	87	17	20%	40	46%	35	88%	19
Paratype, Omaha R.; MCZ	76	15	20%	36	47%	33	92%	18
Mean 2 paratypes, Henderson; MCZ	58	12	21%	28	47%	27	96%	12
Paratype, Kaeo ex Dell	93	18	19%	44	47%	40	91%	21
Paratype, Kaikohe ex Dell	67	12	18%	32	48%	28	88%	15

Material Examined

From Omaha R., Leigh; Creek at Henderson, near Auckland; Kaeo; Kaikohe.

Range

Scattered localities north of Auckland, N.Z.

Genus VIRGUS Simpson

Virgus Simpson, 1900, p. 851. Type species by original designation: *Unio beccarianus* Tapparone Canefri, 1883.

Remarks

This genus was originally proposed for three species of freshwater mussels from the New Guinea region and was claimed by Simpson to be related to the Asian genus *Rectidens*. The three species involved were *Unio beccarianus* Tapp. Can., *U. mattirolii* Tapp. Can., and *Unio misoolensis* Schepman. Haas (1912) considered that *U. misoolensis* did not belong with *Virgus* s.s. and he erected a new subgenus, *Leiovirgus*, for it. He later (1924) maintained the group as a subgenus of *Virgus* and included in it two other species, viz. *Unio guppyi* Smith and *Virgus lorentzi* Schepman.

An examination of available New Guinea material has revealed, as McMichael (1956) has discussed, that *Leiovirgus* belongs with the subfamily Hyridellinae. The genus *Virgus* is thus restricted to the forms first listed by Simpson, the Fly River species *U. beccarianus* and *U. mattirolii*. McMichael considered these two forms to be but variants of a single species; *Virgus* therefore is monotypic.

Diagnosis

Shell Characters.—Freshwater mussels of the subfamily Cucumerunioninae reaching about 100 mm in length. Shells very elongate, very inequilateral, BLI about 15 per cent., MHI about 30–40 per cent., height decreasing markedly towards posterior end. Beaks sculptured with V-shaped ridges continuing posteriorly so that shell surface is strongly sculptured with ridges. Hinge complex with strong grooved cardinal teeth and elongate, low laterals.

Anatomy.—Thiele (1934) gave details of the anatomy of the genus *Virgus* Simpson, but since this was abstracted from Haas's (1924) data on *Leiovirgus*, it cannot be applied to *Virgus*, s.s., the anatomy of which remains unknown.

Glochidium.—Unknown.

Distribution

Fly, Kikori, and Merauke Rivers, New Guinea.

Differential Diagnosis of Species

The genus is monotypic.

Relationships

Virgus is apparently closely related to *Cucumerunio*, from which it differs by being smaller, tapering, relatively more elongate, and possessing a shell sculpture pattern of ridges rather than lachrymose nodules. No fossil species are known.

Virgus beccarianus (Tapparone Canefri)

Plate 16, Figs. 6–9

Unio (*Diplodon*) *beccarianus* Tapparone Canefri, 1883, pp. 291–2, pl. ii, fig. 2.
Unio (*Diplodon*) *mattirolii* Tapp. Can., 1883, pp. 292–3, text fig. 1.
Virgus beccarianus (Tapp. Can.) Simpson, 1900, p. 852; 1914, pp. 1151–2. McMichael, 1956, p. 46.
Virgus mattirolii (Tapp. Can.), Simpson, 1900, p. 852; 1914, pp. 1152–3.
Virgus (*Virgus*) *beccarianus* (Tapp. Can.), Haas, 1912, p. 129, pl. 13, fig. 1; 1924, p. 66.
Virgus (*Virgus*) *mattirolii* (Tapp. Can.), Haas, 1912, p. 131, pl. 13, fig. 2; 1924, p. 66.

Remarks

The two forms listed in the synonymy above, both from the Fly River, New Guinea, have always been maintained as distinct species on the basis of Tapparone Canefri's comments that though both forms showed variability their differences were constant. Haas (1924) viewed them with some doubt, suggesting that, in time, an intermediate form would be found.

McMichael (1956) studied a series of specimens from the Fly River in the Australian Museum, and found that the sculptural details of the shells were quite variable. The series of shells studied was obviously unispecific, and the variability suggested that *exact* sculptural detail was of limited value taxonomically. Since "*beccarianus*" and "*mattirolii*" overlap in shell sculpture, the only basis for maintaining them as separate species would be the greater tumidity and relative shortness of *mattirolii*. As discussed earlier, both of these characters are of questionable value when taken alone. Furthermore, the occurrence of two forms, very similar, in a unique locality, suggests that they are not "good" species. McMichael (loc. cit.) had no hesitation in synonymizing the two, placing *mattirolii* as a junior subjective synonym of *beccarianus*.

Types

The types of *Unio beccarianus* and *U. mattirolii* are, according to Haas (1924), in the Museo Civico di Storia Naturale, Genoa, Italy. Type locality of both: Fly R., Papua, New Guinea.

Description

Shell Morphology.—Shell elongate, maximum length about 100 mm, MHI 25–45 per cent. Anterior portion of shell very short, BLI 10–15 per cent. Anterior margin rounded, somewhat truncated below beaks, cut away ventrally; ventral margin straight or slightly sinuate; dorsal margin scarcely elevated posterior to beaks, then

sloping obliquely towards ventral margin; posterior end of shell produced, posterior margin bluntly truncate. Shells slightly swollen, posterior ridge prominent, separated from posterior slope by a fine ridge, sides of valves rather flattened. Beaks low, not swollen, sculptured with V-shaped ridges, sculpture spreading over posterior surface of shell.

Periostracum olive-brown to reddish brown, darker above posterior ridge. Shell surface sculptured with ridges and nodules, rarely smooth; sculpture consists of ridges running down posterior ridge and spreading dorsally and ventrally. Sculpture development variable, ridges sometimes small and numerous, sometimes strong and few, sometimes poorly developed ventral to posterior ridge, Nacre bluish, iridescent, particularly posteriorly. Shell substance strong but not heavy.

Hinge strong with slender, low lateral teeth, serrated posteriorly; cardinal teeth heavy, jagged, grooved and serrated, often denticulate; cardinals somewhat reduced in old shells. Anterior muscle scars deeply impressed; retractor separate from adductor as a pit under cardinal teeth; posterior scars very lightly impressed; pallial line hardly visible.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
V. beccarianus Holotype, ex Tapp. Can.	76	10	13%	25	33%	21	84%	?
V. mattirolii Holotype, ex Tapp. Can.	55	9	16%	24	44%	22	92%	?
V. beccarianus ex fig. Haas (1912)	76	10	13%	31	41%	27	87%	19
V. mattirolii ex fig. Haas (1912)	56	9	16%	26	46%	22	85%	16
Mean 6 specimens, Fly R.; AM	67	9	13%	21	31%	19	91%	11
1 specimen, Merauke R., Boepoel; AM	100	12	12%	26	26%	23	88%	21

Material Examined

Fly R.; Kikori R. at Middletown; Merauke R., Boepoel; and "British New Guinea" (MZUM).

Range

Fly and Kikori Rivers, Papua, Merauke River, Dutch New Guinea.

Species of Doubtful Validity

(1) "Velesunio ovatus (Haas)"

Microdontia ovata Haas, 1910, p. 100; 1913, p. 161, pl. 16, fig. 5.
Nodularia ovata (Haas), Simpson, 1914, p. 1010.
Hyridella ovata Haas, 1924, p. 71.
Velesunio ovatus (Haas), McMichael, 1956, p. 40.

Remarks

Haas (1910) based this species on two specimens from two collections, neither of which possessed accurate locality data. Haas (1910, 1913) suggested the Fly River, New Guinea, as type locality but later (1924) admitted an error and suggested Konstantinhafen. We have not seen the specimens which Haas studied but the shells closely resemble large specimens of *Velesunio ambiguus* from Australia. Recent collecting by one of us in New Guinea has failed to locate this species and it seems likely that the original material was in fact Australian. While such doubt exists, we prefer not to synonymize "*H. ovata*" with *V. ambiguus* nor to list it as a separate species from the New Guinea region. If it proves to be a valid species, Haas's comments and description suggest that it must be referred to *Velesunio* Iredale.

(2) "Rugoshyria interserta Iredale"

Unio depressus Lamarck, var. *mutabilis* Lea, Hedley and Musson, 1891, p. 564. (Non *Unio mutabilis* Lea, 1859.)
Rugoshyria interserta Iredale, 1934, p. 72, pl. v, fig. 8, pl. vi, fig. 9.

Remarks

This species was based on a unique specimen, recorded many years ago by Hedley and Musson (1891), from Kenilworth, Mary River, Queensland, about 60 miles north of Brisbane. Iredale (1934) related the specimen to *Rugoshyria depressa* (Lam.) (= *Hyridella depressa*) but considered that it was "specifically separable"; his subsequent description was very brief.

The specimen is obviously a species of *Hyridella* and was collected from the extreme northern end of the range of three species of that genus, *H.* (*H.*) *australis*, *H.* (*H.*) *depressa*, and *H.* (*H.*) *drapeta*. It appears to be closer to *H. depressa* than to the others, but differs decidedly in form, particularly in its produced posterior end.

We have examined a reasonable amount of mussel material from the Mary River but have not encountered a shell remotely like "*R. interserta*". Because of its uniqueness, both numerical and morphological, we hesitate to regard it merely as an ecophenotype of *H. depressa* or to recognize it as a valid species. The holotype is in the AM, Reg. No. C. 61949. Type locality: Kenilworth, Mary River, South Queensland.

(3) "Rugoshyria aquilonalis Iredale"

Rugoshyria aquilonalis Iredale, 1934, p. 72, pl. v, fig. 9, pl. vi, fig. 8.

Remarks

Like "*R. interserta*", this species was based on a single specimen, from the Bloomfield River, north Queensland (approx. 16° S. lat., east coast). Iredale (1934) again related it to *R. depressa* (Lam.) (= *Hyridella depressa*) but noted that it was "more compressed, the beaks more anteriorly placed, the ridge more flattened and the anterior end more rounded". He also commented on "traces of shell sculpture" present and thus its possible relationship to *Hyridella guppyi* (Smith) from the Solomon Islands. There is, however, no trace of shell sculpture of the type found in *H. guppyi* and in general facies the specimen resembles *H. depressa*. On the other hand it occurs far to the north of the range of that species and differs from it in

several morphological characters. It may, therefore, represent a northern species or race of *Hyridella*, but we hesitate to locate this specimen in any existing taxon or to regard it as valid on the evidence available.

The holotype is in the AM, Reg. No. C. 484.

Family **UNIONIDAE** Fleming 1828

Freshwater mussels of variable facies, beaks variously sculptured, hinge typically unionid, sometimes reduced; siphons variously developed, a supra-anal usually present; diaphragm complete, formed only by gills; anterior end of inner gills free from palps; marsupium typically in outer or all four gills; larva a glochidium.

Distribution

Europe, Asia, North America, northern South America, Africa, New Guinea (?).

Subfamily **RECTIDENTINAE** Modell

Subfam. Rectidentinae Modell, 1942, p. 189.

Remarks

The subfamily was erected by Modell to include a group of genera placed by him in the family Unionidae. These genera were *Rectidens* Simpson, *Pilsbryoconcha* Simpson, *Pseudanodonta* Bourg., *Lastena* Rafinesque, *Physunio* Simpson, *Ensidens* Frierson, and *Pyganodon* Crosse & Fischer. To these genera, McMichael (1956) added *Haasodonta* McMichael, from New Guinea, this genus being the only non-Australian element in the New Guinea mussel fauna and the only non-mutelid mussel in the Australian Region.

The exact relationship of *Haasodonta* will be known only when its anatomy is known; for the present, its closest relative appears to be *Physunio*.

No formal diagnosis of the subfamily will be given here; Modell (1942) has defined it adequately.

Present Distribution

Northern Europe, North America east of the Rocky Mountains, south-east Asia and New Guinea.

Fossil Record

Known from the Miocene of Bohemia and the Pliocene of Java.

Genus HAASODONTA McMichael

Haasodonta McMichael, 1956, p. 47. Type species by original designation: *Hyridella fannyae* Johnson, 1948.

Remarks

The genus was erected by McMichael (1956) for an aberrant species of mussel from New Guinea, originally placed in *Hyridella*, but bearing no obvious relationship to that genus or any other genus of the Australian Region. At that time, only a single specimen of the type species was known, but now many shells are available,

and one of these differs sufficiently to warrant the erection of a second species, which will necessitate a redefinition of the genus.

Diagnosis

Shell Characters.—Freshwater mussels probably of the subfamily Rectidentinae Modell, of almost anodontine facies. Hinge-line long and straight, almost as long as the greatest length of the shell; hinge simple with elongate, broad lateral teeth, and cardinals variously developed, often elongate and broad; shells compressed anteriorly, swollen posteriorly, particularly along the posterior ridge which is greatly expanded; posterior dorsal margin moderately to strongly winged; periostracum dark brown to black; nacre iridescent posteriorly; shell substance moderately thick.

Anatomy.—Unknown.

Glochidium.—Unknown.

Distribution

Known only from the Merauke River and the Bian River, Dutch New Guinea.

Differential Diagnosis of Species

In *Haasodonta fannyae* (Johnson) the hinge-line is only a little less than, or equal to, the greatest length of the shell, and the dorsal margin is squarely truncate or at an angle less than 90° to the posterior margin. In the new species to be described below (*Haasodonta vanheurni*) the hinge-line is considerably less than the greatest length of the shell, and the dorsal margin is obliquely truncate posteriorly, while the species reaches a larger size.

Relationships

The apparent relationship between *Haasodonta* and *Physunio* has been discussed by McMichael (1956). The discovery of a second species which stands to some extent intermediate between the genus *Alathyria* and *H. fannyae* may indicate that *Haasodonta* is of mutelid stock, derived from *Alathyria* by the expansion of the posterior ridge, possibly in relation to the extremely muddy conditions in which it developed. The true relationship can be confirmed only by anatomical investigation.

Haasodonta fannyae (Johnson)

Plate 16, Figs. 10–12

Hyridella fannyae Johnson, 1948, pp. 47–8, pl. 3, fig. 1.

Haasodonta fannyae (Johnson), McMichael, 1956, pp. 47–8, pl. 2, figs. 3–5.

Remarks

This species was based on a single specimen collected in 1926. Until now, to the best of our knowledge, it has not been collected again. One of us (D.F.M.) was unable to find the species in Merauke, but since then many specimens (dead shells) have been forwarded by E. W. van Heurn from two localities near Merauke. These specimens confirm the fact that this remarkable species is not just a freak, but show that the shells are sometimes even more distorted in form than the holotype.

Types

Holotype MCZ Reg. No. 160663. Type locality: stated to be "Marco River at Merauke", but this should be corrected to Maro or Merauke River, near Merauke. The Maro River is estuarine at Merauke, the species living further up the river.

Description

Shell Morphology.—Shell medium-sized, maximum length about 90 mm, MHI 51–57 per cent. Anterior portion of shell relatively long, BLI 28–33 per cent. Dorsal margin anterior to beaks straight for 10–15 mm, anterior margin rounded, ventral margin markedly sinuate in the middle, the shell considerably deeper posteriorly; dorsal margin posterior to beaks long and straight, then abruptly truncate, at right angles or at an angle less than 90° to the posterior margin; posterior margin long, straight or very slightly sinuate, and continuing smoothly into the rounded and produced postero-ventral margin. Shell outline somewhat axe-shaped. Shell markedly swollen along the posterior ridge, a little compressed in the middle, and with a moderately swollen anterior ridge; posterior slope compressed, antero-dorsal portion of shell compressed; beaks swollen, high, corroded, but apparently without beak sculpture.

Periostracum dark brown to black, marked by fine growth lines and irregular vertical wrinkles of the periostracum on the anterior ridge and anterior side of posterior ridge. Nacre bluish white, iridescent posteriorly, yellowish in beak cavities. Shell substance moderately thick.

Hinge-line long and straight, hinge lamellar; cardinal teeth typically long, low lamellae, sometimes a little thickened and serrated, double in right valve, tending to be double in left, lower tooth the larger, upper occasionally bifurcating, or sometimes reduced altogether. Lateral teeth long and straight, double in left valve, single in right, faintly grooved posteriorly.

Anterior muscle scars deeply impressed, anterior retractor and adductor scars fused; posterior scars and pallial line lightly impressed; beak muscle scars 2 in each valve, deep inside the beak cavity.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	64	20	31%	36	56%	25	69%	38
Mean 10 specimens, Bian R., D.N.G.; AM	75	24	32%	39	52%	28	72%	44
Largest specimen, Bian R.	90	25	28%	45	50%	36	80%	51

Material Examined

As above and from: Boepoel en Kweel, Merauke R., Dutch New Guinea.

Range

Known only from the Merauke and Bian Rivers, southern Dutch New Guinea.

Haasodonta vanheurni, sp. nov.

Plate 19, Figs. 3 and 4

Remarks

As indicated previously, a single shell in the material forwarded by van Heurn differs sufficiently from *H. fannyae*, which appears to be very constant in form, to warrant description as a new species. The locality data for this shell, "Boepoel", together with the locality "Boepoel en Kweel" for two specimens of *H. fannyae* suggests that the two forms are sympatric in the Merauke River at Boepoel. Furthermore, it appears from the data supplied by van Heurn that the local people have different names for the two forms in their language.

Although only a single specimen is available, its form suggests the possibility that *Haasodonta* is derived from an *Alathyria* type shell, so that *H. vanheurni* may represent an intermediate stage in the evolution of the group.

Types

Holotype AM Reg. No. C. 62269. Type locality: Merauke River at Boepoel, Dutch New Guinea.

Description

Shell Morphology.—Shell moderately large, maximum length 112 mm, MHI 47 per cent. Anterior portion of shell relatively long, BLI 25 per cent. Dorsal margin anterior to beaks straight, slightly elevated anteriorly then curving into the evenly rounded anterior margin; ventral margin sinuate in the middle, the shell a little deeper posteriorly; dorsal margin posterior to beaks moderately long, straight, then obliquely truncate at an angle of about 55°; postero-ventral margin evenly rounded and a little produced. Shell noticeably swollen along the posterior ridge, but not as much as in *H. fannyae*; compressed medially, the anterior ridge a little expanded; posterior slope compressed; beaks swollen, high, corroded.

Periostracum dark, marked by fine growth lines. Nacre bluish white or white, iridescent posteriorly, yellowish under the beaks. Shell substance moderately thick.

Hinge long, slightly curved; cardinal teeth thickened lamellae, double in the right valve, the upper tooth almost completely reduced, single in the left, the teeth faintly grooved and serrated. Lateral teeth very long and straight, broad lamellae, double in left valve, single in right.

Anterior muscle scars deeply impressed, anterior retractor and adductor scars fused; posterior scars and pallial line very light. Beak muscle scars 5 in a row deep inside the beak cavity.

Anatomy.—Unknown.

Glochidium.—Unknown.

Dimensions (all lengths in mm)

Specimen	L	BL	BLI	MH	MHI	BH	BHI	W
Holotype	112	28	25%	53	47%	41	77%	51

Material Examined

Holotype only.

Range

Known only from the type locality.

IV. Distribution and Phylogeny

(*a*) *Distribution*

Freshwater mussels occur in the majority of permanent habitats on the mainland of Australia, northern Tasmania, New Guinea, and both islands of New Zealand. In continental Australia, the majority of species occurs in the well-watered eastern half of the continent. In general, as Iredale (1943*b*) has pointed out, distribution of species is determined more or less by the geography of the river systems. The occasional irregularities in distribution are due, probably, to accidental transfer of mussels from river to river by birds. The agreement of distribution and river systems applies to freshwater faunas generally in Australia, and as a result, a series of zoogeographical provinces with characteristic fluvifaunulae can be recognized, based largely on the major river drainage systems. These river systems are as follows: (1) eastern coastal drainage system consisting of streams from Cape York south to western Victoria draining generally eastwards from the Great Dividing Range; the principal rivers of Tasmania are essentially a part of this same system; (2) Murray–Darling system draining largely westward from the Dividing Range, the Darling River and tributaries draining northern New South Wales and southern Queensland, the Murray River and tributaries draining southern New South Wales and northern Victoria; (3) Bullo Basin with the isolated Bulloo River, probably once associated with the Darling River; (4) Lake Eyre drainage consisting of inland streams from mid western Queensland and Central Australia, many only rarely connecting with Lake Eyre and frequently almost dry; (5) coastal drainage of the south of Western Australia, extending from about Esperance to a little north of Perth, consisting of fairly permanent streams draining from the Darling and Stirling Ranges; (6) mid Western Australian coastal drainage of intermittent streams from Geraldton north to Ninety-Mile Beach; (7) north Western Australian coastal drainage of variable streams north from Ninety-Mile Beach to Van Diemen Gulf, draining mainly from the King Leopold and Durack Ranges; (8) Gulf drainage system of coastal rivers entering the Gulf of Carpentaria, draining northwards from the Barkly Tableland and, in Cape York Peninsula, westwards from the Great Dividing Range.

Differences in the freshwater faunas, particularly fish and molluscs, of these main river systems were studied by Iredale and Whitley (1938) who proposed a series of names for the fluvifaunulae found in them. Both authors (Iredale 1943*a*; Whitley 1947) later proposed minor modifications of their original scheme which however retained its original broad outlines. The following discussion of these faunistic provinces is confined to freshwater mussels and the relation of their distribution to the provinces in the light of the findings of the present work.

The Lessonian fluvifaunula, occupying the southern half of the east coast drainage system, is characterized by the genus *Hyridella*, two subgenera (*Hyridella* and *Protohyridella*) being represented. The region has been penetrated by *Cucumerunio* and *Alathyria p. pertexta* from the north and *Velesunio* from inland, but none of these is characteristic. *Alathyria profuga* is confined to a small part of the region and cannot therefore be considered characteristic.

The Tobinian fluvifaunula occupies the rivers of southern Tasmania and no freshwater mussels are included in it.

The Krefftian fluvifaunula occupies the coastal streams of the east coast of Queensland from about Brisbane north to the Tropic of Capricorn. Two species of mussels, *Alathyria p. pertexta* and *Cucumerunio novaehollandiae*, are characteristic. *Velesunio ambiguus* has penetrated from inland through most of the area and *Hyridella* from the Lessonian fluvifaunula occurs in the southern part.

The Jardinian fluvifaunula was originally defined as that occupying the rivers of the east coast of Queensland north of the Fitzroy River to Cape York and the rivers of the west coast of Cape York Peninsula. Whitley (1947) modified this scheme slightly, placing the faunas of the west coast streams into the Leichhardtian province. The distribution of freshwater mussel species confirms Whitley's modification, the species of the west coast streams being definitely Leichhardtian. There are no characteristic mussel species in the Jardinian fluvifaunula, but *V. ambiguus* and *V. wilsonii* have penetrated from inland.

The Leichhardtian fluvifaunula, with the above modification, extends across the north of the continent from the Kimberley region in the west (north-western coastal drainage) to the east, incorporating the Gulf drainage system. *Velesunio angasi* is the characteristic species with *V. wilsonii* penetrating from the south into the Gulf drainage streams and appearing again in the north-west. The aberrant *Lortiella* is characteristic of the north-west sector, and a subspecies of *Alathyria pertexta*, *A. p. wardi*, occurs in a few streams of the Gulf drainage.

The Vlaminghian fluvifaunula, which occurs in the south-western drainage system, is a very characteristic assemblage. The only freshwater mussel species present is *Westralunio carteri*, a distinct species confined to that region.

The mid-western drainage streams are inhabited by the Greyian fluvifaunula. Iredale and Whitley (1938) listed *Lortiella* as the characteristic mussel of this region, but the only known records of that genus are from the north-western streams in the Leichhardtian province. As Whitley (1947) has pointed out, the Greyian region is to be considered unexplored from the point of view of the naturalist. At present, no freshwater mussels are known from the region.

The Mitchellian fluvifaunula occupies the Murray–Darling river system. The characteristic mussels are velesunionine mussels, *Velesunio ambiguus* and *Alathyria jacksoni* being abundant throughout the system. The Bulloo River system is included in this region.

The Sturtian fluvifaunula is here considered to occupy only the Lake Eyre drainage system and not any of the Gulf drainage streams, which are placed here in the Leichhardtian region. The characteristic mussel species occurring in the Sturtian fluvifaunula is *Velesunio wilsonii*, which, as outlined above, is not confined to this region.

The mainland of New Guinea possesses two distinct fluvifaunulae, occurring on opposite sides of the central mountain system. Iredale and Whitley (1938) considered that the Leichhardtian fluvifaunula of northern Australia extended to southern New Guinea. However, with the exception of one subspecies, *Alathyria pertexta magnifica*, from Merauke, Dutch New Guinea, there are no mussel species common to both regions. Southern New Guinea possesses a number of very distinct species, including

Hyridella (*H.*) *misoolensis*, *Westralunio flyensis*, and *Microdontia anodontaeformis*. In addition there are two endemic genera, *Virgus* and *Haasodonta*. We feel that this fluvifaunula is sufficiently distinct to warrant a separate name and propose to call it the Riechian fluvifaunula, in honour of Dr. E. Riech who pioneered the study of distribution of freshwater molluscs in this region.

The northern New Guinea drainage is characterized by the Gaimardian fluvifaunula and a single mussel species, *Velesunio sentaniensis*, is characteristic.

The limits of distribution of the several fluvifaunulae are shown in Figure 17.

Fig. 17.—The fluvifaunal provinces of Australasia (modified from Iredale and Whitley 1938). 1, Lessonian; 2, Tobinian; 3, Krefftian; 4, Jardinian; 5, Leichhardtian; 6, Vlaminghian; 7, Greyian; 8, Mitchellian; 9, Sturtian; 10, Gaimardian; 11, Riechian.

The distribution of the New Zealand freshwater mussels does not appear to have reached stability at present. The three species present are probably of fairly recent origin and the present drainage systems of the country also appear to be relatively young.

(*b*) *Phylogeny*

(1) *Higher Classification.*—As a prerequisite to a consideration of the phylogeny of the Australasian species of freshwater mussels, the relationships of these mussels to those of the rest of the world must be considered. Since the higher classification of the group generally has never reached stability, it is necessary also to review briefly the several systems of classification proposed and to evaluate their applicability to the fauna under present review.

The earliest attempts at classification of freshwater mussels, such as those of Swainson (1840), Gray (1847), and Lea (1870), were based on purely superficial

resemblances between shells of species from all over the world and disregarded any zoogeographical considerations. Agassiz (1852) was the only early worker to attempt to use anatomical characters, but he was misled, also, by superficial resemblances.

Simpson's (1896, 1897, 1900, 1914) classification, based on conchological and anatomical considerations, recognized two families, Unionidae and Mutelidae. The Unionidae were characterized by a hinge with schizodont teeth and a glochidium as the larval stage and included most of the North American, Eurasian, south-east Asian, and Australasian genera and some African forms. The Mutelidae possessed taxodont hinge teeth and a lasidium larva, and included some South American and African genera thought to possess these characters. The family Unionidae was subdivided into two subfamilies: Unioninae, with concentric beak sculpture and embryos in all four or outer gills only and Hyriinae with radial beak sculpture and marsupia in the inner gills only. Within the Hyriinae, Simpson grouped all of the Australian and New Zealand species (except *Lortiella rugata*, placed under Mutelidae) in the genus *Diplodon* which also included South American and African species. *Hyridella* was used subgenerically for the Australian and New Zealand forms, the subgeneric characters including "sculpture consisting of curved, generally modulous ridges which approach below . . .". With the exception of *Westralunio flyensis* which he placed under *Diplodon*, Simpson related the New Guinea species known at the time to south-east Asian unionids.

Simpson's system failed for the following reasons: (1) his basic subdivision on hinge characters was unsound, this structure being most susceptible to adaptation and convergence; (2) his simple concept of beak sculpture was inadequate to account for the patterns which occur; (3) he was unaware of the real significance of the differences in anatomical characters between his two subfamilies of the Unionidae; and (4) his use of larval types as a basis for subdivision stemmed largely from supposition.

With regard to the Australasian groups, Simpson assumed that all possessed radial beak sculpture, a belief that Frierson (1908) showed to be erroneous, noting that one species possessed unsculptured beaks and was "strictly speaking . . . not even a *Diplodon*". Frierson suggested broadening the diagnosis of *Diplodon* and segregating the species he had studied, as well as some other Australian species, subgenerically.

Ortmann (1909, 1910, 1911*a*, 1911*b*, 1911*c*) proposed a scheme of classification which, in contrast to Simpson's, was based almost entirely on anatomical characters. The details of Ortmann's basis of classification need not be discussed here, but in broad outline his scheme recognized the following groups: (*a*) Unionidae proper, separated to three subfamilies: (i) Unioninae, the most primitive, with marsupia in all four or only the outer gills and without secondary water tubes, (ii) Anodontinae, with marsupia in the outer gills only and with secondary water tubes, and (iii) Lampsilinae, the most highly developed, with marsupia in the outer gills, frequently restricted, and without secondary water tubes, all three subfamilies having glochidia as larvae. (*b*) Mutelidae, with marsupia in the inner gills only, separated to (i) Mutelinae with continuous septa in the marsupium and a lasidium larva and (ii) Hyriinae (= Simpson's group of the same name) with discontinuous septa in the marsupium

and a glochidium larva. (It should be noted that the use of the names Mutelidae and Mutelinae was based on assumption, the anatomy of the genus *Mutela* being unknown.) (*c*) Margaritanidae, supposedly the most primitive of all living freshwater mussels, possessing an incomplete diaphragm, marsupia in all four gills, and glochidia of the small, semicircular, hookless type.

Ortmann (1912, 1920*a*) studied some specimens of the Australian species, *Velesunio ambiguus*, clearly established its relationship to the South American Mutelids (Hyriinae) and suggested that the Australian mussels deserved generic rank separate from *Diplodon* to which Simpson had assigned them. Ortmann's findings in this regard have been discussed in detail in Section II(*a*)(ii).

Ortmann's classification at the level of the higher taxa became generally accepted and for some years, taxonomic research on freshwater mussels involved only the lower taxa. The only works of significance to the Australian Region were Haas's (1924, 1930) studies, which clearly related the New Guinea mussels to the Australian and New Zealand groups and not to the south-east Asian genera as Simpson had suggested.

Iredale (1934) reviewed the Australian species and proposed to separate them in a new family, Propehyridellidae, on the grounds (1) that some lacked beak sculpture and (2) "the absence of a hooked glochidium stage". No anatomical studies were made on the group. Iredale's grounds for the erection of a new family are unacceptable because, firstly, the Australian forms produce a glochidium (a fact noted much earlier by Tenison-Woods (1888)) and, secondly, the absence of beak sculpture was recognized in some of the genera in Ortmann's subfamily Mutelinae. The four subfamilies which Iredale recognized in his "Propehyridellidae" have been used in the present work, for reasons discussed below.

Modell (1942) in Part 1 of his "natürliche System der Najaden", worked from a completely different viewpoint from previous authors. Modell believed that the basic, phylogenetically useful character was beak sculpture and that the form of the shell and hinge, many anatomical characters (including the position of the marsupium), and larval type were useful only to a limited extent. Modell's system admitted four families as follows: (i) Mutelidae, primitive living forms, divided to 15 subfamilies, including most of the African and South American groups and the Velesunioninae and Lortiellinae of Australia, (ii) Elliptionidae, a new family, confined to North America, including six subfamilies, embracing genera from all three of Ortmann's subfamilies of Unionidae, (iii) Margaritiferidae (= Ortmann's Margaritanidae) with four subfamilies including the Australasian Cucumerunioninae and a number of Eurasian genera, and (iv) Unionidae, with two subgroups, representing two separate lines of development of beak sculpture, embracing 14 subfamilies, including the Australian Hyridellinae, the Hyriinae of Ortmann (restored to the group again), and most of the genera in Ortmann's Unioninae and Anodontinae. Of the total number of 39 subfamilies, 27 were new.

In Part 2 of his system, Modell (1949) gave anatomical data to support his concepts and, in addition, erected a new "family" for the Mutelidae of his original system which retained a primitive lamellar hinge, thus including the Velesunioninae. He called this family Austromutelidae, but no genus existed on which such a name

could be based. Since we do not recognize the validity of the group, we do not propose to replace the name.

Modell incorporated a great deal of fossil evidence into his original system, but to what extent the fossils can be adequately determined is doubtful.

Of the Australian groups, Modell thought the Velesunioninae to be very primitive, among the most primitive forms known, with the Lortiellinae an early offshoot of this old mutelid stock. He regarded the Margaritiferidae and Unionidae as having arisen from the Mutelidae in the Indo-Pacific, the Margaritiferidae being represented in Australia by its most primitive group, the Cucumerunioninae, while the Unionidae reinvaded Australia as Hyridellinae and moved into South America as Hyriinae, thus explaining the similarity of these groups.

The applicability of these several schemes of classification to the Australasian groups recognized here can now be considered.

The five subfamilies recognized in the present work are at a somewhat different level from the subfamilies of Simpson and Ortmann. But they are clear-cut groups in Australasia, each representing an assemblage of closely allied genera. The Lortiellinae are possibly close to the Velesunioninae but until the anatomy of *Lortiella* is known the question cannot be settled. The Cucumerunioninae are probably close to the Hyridellinae, their anatomy being quite similar and their beak sculpture being basically the same. The genus *Haasodonta*, placed here in the Unionidae, subfamily Rectidentinae Modell, is conchologically quite distinct from any other group in the region.

The present work has revealed an overall similarity in the anatomy of three of the first four subfamilies, with a recognizable dichotomy between the Velesunioninae on the one hand and the Hyridellinae and Cucumerunioninae on the other. Hinge structure and beak sculpture support this view. This suggests at least two separate origins for the Australasian fauna, their basic similarity suggesting either two closely related ancestral groups or separate origins from the same stock at different time intervals.

Simpson's classification obviously will not apply here, since his scheme did not recognize the distinction between these two groups. The Velesunioninae are similar anatomically to the *Diplodon*-like genera of South America (Hyriinae) but the lack of beak sculpture and some anatomical differences noted by Ortmann (1912) suggest that the relationship is not close. The Hyridellinae, on the other hand, appear superficially to be fairly closely related to the South American Hyriinae.

Ortmann's scheme is unsatisfactory because it likewise does not recognize the fundamental divergence in the Australian forms.

Modell's scheme, taking into account the several Australian forms, is more satisfactory, but the separation of subfamilies is too great, the Velesunioninae, Hyridellinae, and Cucumerunioninae all being placed in separate families on the basis of sculptural characters. As mentioned above, Modell placed far less stress on anatomical features in his classification and was unaware of the close, basic anatomical similarity between the Velesunioninae, Hyridellinae, and Cucumerunioninae. Even if we allow Modell's view that certain anatomical characters, particularly the

marsupium, are subject to rapid selection, Ortmann's studies make it clear that certain fundamental anatomical differences exist in freshwater mussels that cannot represent the result of repeated and rapid selection and adaptation. The similarity in the Australasian groups is too great to admit of widely separate origins in this way.

Except for *Haasodonta*, the Australasian groups are definitely separable from the true Unionidae and the true Margaritiferidae. Their relationships appear to lie with the South American Mutelidae. If they are to be considered as belonging to one descrete unit, they do not fit easily to either of Ortmann's subfamilies nor can they be accommodated by Modell's subfamilies within this family. Nor do they warrant the erection of a separate family to accommodate them.

Of the several possible ways of dealing with higher taxa for the group, we have chosen the one used above, i.e. retaining Iredale's scheme of allotting the several groups subfamily status. This seems quite feasible as far as the Velesunioninae and Hyridellinae are concerned, but whether the Lortiellinae deserve such status is unanswerable at present and the Cucumerunioninae may be more closely related to the Hyridellinae than their subfamily status suggests. More detailed knowledge of the anatomy and larval stages of the many forms still unexamined will throw light on the problem.

(ii) *Phylogenetic Considerations.*—It is impossible to draw any definite conclusions on the origin of the Australasian freshwater mussel fauna from the fossil evidence available for the group. As well as upon palaeogeographic information, it is necessary, therefore, to draw upon evidence of present relationships, bearing in mind zoogeographical data derived from the study of other groups of animals.

The group from which freshwater mussels arose is not yet known but the generally accepted possibilities are the families Trigoniidae and Anthracosiidae, the weight of evidence favouring the latter. The Anthracosiidae were abundant in freshwater in the middle Palaeozoic in the northern hemisphere and apparently became extinct at the end of the era. No definite fossil material of the group has been discovered as yet from the Australian Region.

Modell's findings suggest that the most primitive, and presumably earliest, freshwater mussels were mutelids, apparently widely distributed as fossils from the late Palaeozoic in the northern hemisphere, but not extending beyond the Mesozoic in those regions, except for a doubtful Pliocene lortielline shell from China. The mutelids are now represented as living forms only in the southern hemisphere, in the Neotropical, Ethiopian, and Australian Regions. These three faunas may have invaded these regions from the north, possibly during the early Mesozoic.

The earliest fossil "mussel" from the Australian Region is "*Anodonta*" *gouldii* Johnston from the Fingal slates of Tasmania. As McMichael (1957) has pointed out, the age of these beds, according to David (1950), is either Upper Silurian or Lower Devonian, rather early for a true freshwater mussel, and the "species", known only from a figure, is of very doubtful affinity.

If we presume that the sculptureless forms represent the primitive mutelids, it is expected that such forms would appear earliest in the fossil record for any region with fossil mussels dating to the early Mesozoic. Such is precisely the case in Australasia, *Prohyria eyrensis* (Etheridge Jr.) appearing in Australia in the Triassic.

This species is probably a velesunionid, which family is considered to be the most primitive of the Region. This family has persisted as a very stable group to the present time. The origin of the group in Australia was possibly from south-east Asia in the north.

The other Mesozoic mussels known from Australia, except for *Velesunio jaqueti* (Newton) from the Cretaceous, are of doubtful affinity.

The first freshwater mussel of the region which can be definitely related to a present-day group other than the Velesunioninae is *Hyridella whitecliffsensis* (Newton) from the Cretaceous of New South Wales, belonging to the subfamily Hyridellinae and to a genus which has persisted to the present day. No other *Hyridella* species appear as fossils until the late Tertiary. Since Australia has been isolated from south-east Asia since the late Mesozoic, it seems that the Hyridellinae, and (in the absence of fossil evidence to the contrary) the Cucumerunioninae, evolved in Australia from primitive (velesunionid ?) stock. Such an evolution would explain the unity of the mussels of the region.

The Hyridellinae have developed the sculpture of the true Unionidae, while the Cucumerunioninae have assumed a margaritiferid form, but anatomically both groups are more closely allied to the Velesunioninae and thus to the Mutelidae than to any other family. This apparent convergence led Modell to assign them to the families which they most resembled in external form.

As suggested previously the relationship of the Lortiellinae is uncertain. They may be related to the mycetopodine mussels of Asia or they may be early derivatives of the Velesunioninae.

The genus *Haasodonta* (subfamily Rectidentinae) is apparently a comparatively late derivative of south-east Asian members of that subfamily, but little is known about its morphology and distribution. As discussed above, it is conceivably related to the velesunionid *Alathyria*.

The evolution of the genera within the Australian Region cannot be traced adequately on existing fossil data. From what is known (see McMichael 1957), the following tentative suggestions can be put forward.

The genus *Velesunio* is apparently the oldest and most primitive in the region, dating back to the Triassic. *Alathyria*, at the present time very similar to *Velesunio*, is not known from fossil material until the Tertiary, *A. tamarensis* (Etheridge Jr.) being recorded from the Oligocene of Tasmania. *Alathyria* is almost certainly a derivative of *Velesunio* but the fossil evidence available does not warrant speculation on its age. *Westralunio* is another probable derivative of *Velesunio* but its age is unknown. It has been isolated geographically in Western Australia at least since the Miocene.

Microdontia, though almost certainly a velesunionid, is rather different morphologically from *Velesunio*, and may be a very old derivative of it.

Lortiella, as discussed above, is of uncertain affinity but it would appear to be either an early derivative of *Velesunio* or a later offshoot of a south-east Asian stock.

The Hyridellinae, which in Australia are of limited distribution, are anatomically close to the Velesunioninae and were probably derived from them late in the Mesozoic.

It is probable that prolonged isolation under rather different ecological conditions from their ancestors resulted in their characteristic beak sculpture.

The Cucumerunioninae unfortunately have no known fossil representation, but probably arose from hyridelline stock. The genus *Virgus*, apparently related to *Cucumerunio*, is sufficiently different morphologically to suggest that it diverged early from *Cucumerunio* stock. These possible evolutionary relationships are shown in Figure 18.

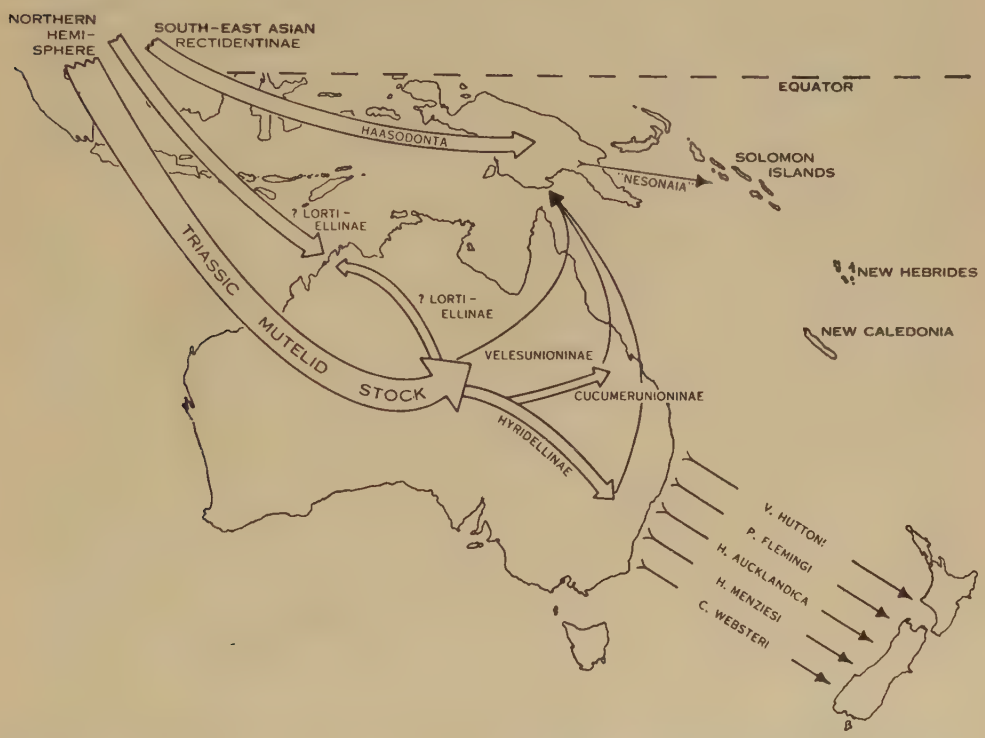

Fig. 18.—Suggested origin and phylogeny of the freshwater mussels of the Australian Region. The open arrows refer to the origins of major groups, the finer arrows to subsequent distributions of the several groups.

The origin of the New Zealand fauna has generally been assumed to be closely linked with that of Australia and to have been derived either via a southern continental connection between South America and both Australia and New Zealand, or via a northern route from New Guinea and the Solomon Islands. Ihering (1891*b*), Simpson (1896, 1897, 1900, 1914), and Beaufort (1951) have supported the southern land bridge concept to account for the similarity of the fauna of the two regions. There is very little possibility of any direct land connection between Australia and New Zealand or between New Zealand and New Guinea in comparatively recent times. If such land connections did exist, it is reasonable to suppose that groups besides mussels, such as mammals and modern reptiles, would have traversed the same route. The absence of freshwater mussels from New Caledonia would not be expected had

migration taken place along a northern land connection which would presumably have included that island.

As far as New Zealand is concerned, McMichael (1958) has discussed the probable origin of its freshwater mussel fauna, favouring bird transfer. As Falla (1953) has noted, several Australian water birds, but no New Guinea species, regularly appear in New Zealand. This suggests an Australian origin for the New Zealand mussels. Only five successful introductions from Australia would be necessary to account for the known New Zealand species, viz. (1) a Mesozoic transfer of *Protovirgus* stock to account for the upper Cretaceous *P. flemingi* McMichael, (2) one transfer of *Velesunio* stock to give rise to the Tertiary *V. huttoni* McMichael, (3 and 4) two transfers of *Hyridella* stock giving rise to the present day *Hyridella* (*H.*) *aucklandica* and *H.* (*Echyridella*) *menziesi*, the latter two being sufficiently different from each other to suggest separate origins, and (5) one transfer of *Cucumerunio* stock to give rise to *C. websteri*.

A full discussion of this matter has been given by McMichael (1958).

The origin of the Solomon Islands species, *Hyridella* (*Nesonaia*) *guppyi*, was almost certainly similar to that of the New Zealand forms. Its absence from the islands between the Solomons and New Guinea does not support a land bridge origin as suggested by Riech (1937). The similarity between the freshwater mussel faunas of Australasia and South America has been a subject of considerable interest to zoogeographers. In the preceding remarks, we have adopted the view that this similarity is due to a common northern origin and subsequent restriction of the group to the southern continents since the early Mesozoic. The maintenance of this similarity may have been due to, firstly, the evolutionary stability of the faunas in question, as instanced by the geological antiquity of the Velesunioninae in Australia, and, secondly, a certain amount of parallelism in the evolution of the present-day representatives. Thus, in Australia, two major groups of mutelids have developed, the velesunionine and hyridelline forms; in South America, their counterparts are to be found in the Mutelinae and Hyriinae respectively.

However, most other authors (Ihering 1891*b*; Beaufort 1951) have preferred to account for the similarity in terms of a common southern origin, and this point of view cannot be disregarded as there is a good deal of supporting evidence in other animal and plant groups.

Whatever its origin, it must be stressed again that, with the exception of *Haasodonta*, the freshwater mussel fauna of the Australian Region forms a well-defined unit. Its distribution, like that of the majority of the Australo-Papuan fauna, is limited by a line along the edge of the Sahul Shelf (Mayr 1944). To the west of this line exists a predominantly unionid mussel fauna, having no close relationship with the Australasian forms.

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EXPLANATION OF PLATES 1–19

The abbreviations used below are those explained in the text (p. 385), and RNHL = Rijksmuseum van Natuurlijke Historie, Leiden; DPUQ = Department of Photography, University of Queensland. The institutions thus abbreviated are the sources of the photographs used and are not necessarily the parent institutions of the specimens. Where no acknowledgment is given, the photographs are the authors' own.

PLATE 1

Velesunio ambiguus (Philippi)

Figs. 1 and 2.—*Unio ambiguus* Philippi: Holotype, BM. ×⅔.
Figs. 3–5.—*Unio jeffreysianus* Lea: Holotype, USNM. ×⅔.
Figs. 6 and 7.—*Unio evansi* Adams & Angas: Holotype, BM. ×⅔.
Figs. 8 and 9.—*Unio balonnensis* Conrad: Holotype, ANSP. ×⅔.
Fig. 10.—*Velesunio mckeowni* Iredale: Holotype, AM. ×⅔.
Figs. 11 and 12.—*Velesunio balonnensis intricatus* Iredale: Holotype, AM. ×⅔.
Figs. 13 and 14.—*Unio vittatus* Lea: Paratype, USNM. ×⅔.

Plate 2

Velesunio ambiguus (Philippi): Figs. 1–5
Velesunio legrandi (Petterd): Figs. 6 and 7
Velesunio wilsonii (Lea): Figs. 8–11

Fig. 1.—*Unio vittatus* Lea: Holotype, BM. ×⅔.
Fig. 2.—*Velesunio balonnensis adjunctus* Iredale: Holotype, AM. ×⅔.
Figs. 3 and 4.—*Velesunio transitus* Iredale: Lectotype, AM. ×⅔.
Fig. 5.—*Velesunio testatus* Iredale: Holotype, AM. ×⅔.
Fig. 6.—*Unio legrandi* Petterd: Holotype, AM. ×⅔.
Fig. 7.—*Velesunio legrandi* (Petterd): Adult specimen, Liffey R. Tas.; DPUQ. ×⅔.
Figs. 8 and 9.—*Unio wilsonii* Lea: Holotype, ANSP. ×1⅓.
Figs. 10 and 11.—*Unio stuarti* Adams & Angas: Holotype, BM. ×⅔.

Plate 3

Velesunio wilsonii (Lea): Figs. 1–3
Velesunio angasi (Sowerby): Figs. 4–12

Fig. 1.—*Centralhyria wilsonii caurina* Iredale: Holotype, AM. ×⅔.
Fig. 2.—*Velesunio wilsonii* (Lea): Maro R., Merauke, Dutch New Guinea; MCZ. ×⅔.
Fig. 3.—*Velesunio wilsonii* (Lea): Adult specimen, Aramac Ck., Aramac, Qld.; DPUQ. ×⅔.
Figs. 4 and 5.—*Unio angasi* Sowerby: Holotype, BM. ×⅔.
Figs. 6 and 7.—*Aparcthyria hemesa* Iredale: Holotype, AM. ×⅔.
Figs. 8 and 9.—*Hyridella bardwelli* Clench: Holotype, MCZ. ×⅔.
Figs. 10–12.—*Quaesithyria fleckeri* Iredale: Lectotype, AM. ×⅔.

Plate 4

Velesunio angasi (Sowerby): Figs. 1–6
Velesunio sentaniensis (Haas): Figs. 7–10
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Figs. 1 and 2.—*Unio bednalli* Tate: Holotype, SAM. ×⅔.
Fig. 3.—*Aparcthyria inspecta* Iredale: Paratype, AM. ×⅔.
Figs. 4 and 5.—*Aparcthyria inspecta* Iredale: Holotype, AM. ×⅔.
Fig. 6.—*Anodon angasii* Sowerby: British Museum Specimen, BM. ×⅔.
Figs. 7*A* and 8.—*Velesunio sentaniensis* (Haas): Hollandia, Dutch New Guinea, MCZ. ×⅔.
Fig. 7*B*.—*Velesunio sentaniensis* (Haas): Aitape, New Guinea, MCZ. ×⅔.
Fig. 9.—*Velesunio sentaniensis* (Haas): Lae, New Guinea. ×1.
Fig. 10.—*Hyridella sentaniensis* Haas: Australian Museum Paratype, AM. ×1.
Figs. 11 and 12.—*Microdontia anodontaeformis* (Tapparone Canefri): Topotype, AM. ×⅔.

Plate 5

Alathyria jacksoni Iredale

Figs. 1 and 2.—*Alathyria jacksoni* Iredale: Holotype, AM. ×⅔.
Figs. 3 and 4.—*Alathyria selwyni* Iredale: Holotype, AM. ×⅔.
Fig. 5.—*Alathyria jacksoni alleni* Iredale: Holotype, AM. ×⅔.

PLATE 6

Alathyria pertexta pertexta Iredale: Figs. 1–4

Alathyria pertexta wardi Iredale: Fig. 5

Figs. 1 and 2.—*Unio shuttleworthi* Lea: Holotype, USNM. ×⅔.
Fig. 3.—*Alathyria pertexta* Iredale: Holotype, AM. ×⅔.
Fig. 4.—*Alathyria morti* Iredale: Holotype. AM. ×⅔.
Fig. 5.—*Quaesithyria wardi* Iredale: Lectotype, AM. ×⅔.

PLATE 7

Alathyria profuga (Gould): Figs. 1–4

Alathyria condola Iredale: Figs. 5–7

Figs. 1 and 2.—*Unio profugus* Gould: Holotype, USNM. ×⅔.
Fig. 3.—*Alathyria vadena* Iredale: Holotype, AM. ×⅔.
Fig. 4.—*Alathyria profuga* (Gould): Adult specimen, Williams R., Dungog, N.S.W.; AM. ×⅔.
Fig. 5–7.—*Alathyria condola* Iredale: Holotype, AM. ×⅔.

PLATE 8

Westralunio carteri Iredale: Figs. 1–7

"Membridge River" shell: Figs. 8–10

Westralunio flyensis (Tapparone Canefri): Figs. 11–14

Westralunio albertisi Clench: Figs. 15 and 16

Figs. 1–4.—*Westralunio carteri* Iredale: Lectotype, AM. ×⅔.
Fig. 5.—*Westralunio carteri* Iredale: Adult specimen, Bow R., W.A.; AM. ×⅔.
Figs. 6 and 7.—*Centralhyria angasi subjecta* Iredale: Lectotype, BM. ×⅔.
Figs. 8–10.—*Velesunio ambiguus* (Philippi)?: "Membridge River" shell, BM. (See text.) ×⅔.
Figs. 11–14.—*Westralunio flyensis* (Tapparone Canefri): Topotype, AM. ×⅔.
Fig. 15.—*Westralunio albertisi* Clench: Holotype, MCZ. ×⅔.
Fig. 16.—*Westralunio albertisi* Clench: Australian Museum Paratype. ×⅔.

PLATE 9

Lortiella rugata (Sowerby): Figs. 1 and 2

Lortiella froggatti Iredale: Figs. 3–5

Hyridella (*Hyridella*) *australis* (Lamarck): Figs. 6–18

Figs. 1 and 2.—*Mycetopus rugatus* Sowerby: Lectotype, BM. ×⅔.
Figs. 3 and 4.—*Lortiella froggatti* Iredale: Holotype, AM. ×⅔.
Fig. 5.—*Lortiella froggatti* Iredale: Paratype, AM. ×⅔.
Figs. 6–8.—*Unio australis* Lamarck: Lectotype, MNHN. ×⅔.
Figs. 9–11.—*Unio australis* Lamarck: Paratype, MNHN. ×⅔.
Figs. 12 and 13.—*Unio nepeanensis* Conrad: Holotype, ANSP. ×1⅓.
Figs. 14 and 15.—*Unio lessoni* Kuster: Holotype, USNM. ×⅔.
Figs. 16–18.—*Unio dorsuosus* Gould: Holotype, USNM. ×⅔.

Plate 10

Hyridella (*Hyridella*) *australis* (Lamarck): Figs. 1–6
Hyridella (*Hyridella*) *drapeta* (Iredale): Figs. 7–13

Figs. 1 and 2.—*Propehyridella nepeanensis opportuna* Iredale: Holotype, AM. ×⅔.
Fig. 3.—*Hyridella* (*H.*) *australis* (Lamarck): Mitchell R., Bairnsdale, Vic.; AM. ×⅔.
Figs. 4–6.—*Propehyridella nepeanensis novata* Iredale: Holotype, AM. ×⅔.
Figs. 7 and 8.—*Hyridunio australis drapeta* Iredale: Holotype, AM. ×⅔.
Figs. 9 and 10.—*Hyridunio renutus* Iredale: Holotype, AM. ×⅔.
Figs. 11 and 12.—*Hyridunio australis orion* Iredale: Lectotype, AM. ×⅔.
Fig. 13.—*Hyridunio australis casus* Iredale: Holotype, AM. ×⅔.

Plate 11

Hyridella (*Hyridella*) *depressa* (Lamarck)

Figs. 1–5.—*Unio depressa* Lamarck: Holotype, MNHN. ×1.
Figs. 6–8.—*Unio paramattensis* Lea: Holotype, USNM. ×1.
Figs. 9 and 10.—*Unio mutabilis* Lea: Paratype, USNM. ×1.
Fig. 11.—*Unio mutabilis* Lea: Paratype, BM. ×1·4.

Plate 12

Hyridella (*Hyridella*) *depressa* (Lamarck): Figs. 1–6
Hyridella (*Hyridella*) *narracanensis* (Cotton & Gabriel): Figs. 7–12
Hyridella (*Hyridella*) *aucklandica* (Gray): Figs. 13–17

Figs. 1 and 2.—*Rugoshyria depressa vicinalis* Iredale: Lectotype, AM. ×⅔.
Fig. 3.—*Rugoshyria depressa bega* Iredale: Holotype, AM. ×⅔.
Figs. 4 and 5.—*Rugoshyria depressa monticola* Iredale: Holotype, AM. ×⅔.
Fig. 6.—*Rugoshyria depressa lowanna* Iredale: Holotype, AM. ×⅔.
Figs. 7–9.—*Propehyridella narracanensis* Cotton & Gabriel: Holotype, NMV. ×1⅓.
Fig. 10.—*Propehyridella narracanensis* Cotton & Gabriel: Paratype (Birregurra), DPUQ. ×1⅓.
Figs. 11 and 12.—*Hyridella* (*H.*) *narracanensis* (Cotton & Gabriel): Adult, Liffey R., Tas.; DPUQ. ×⅔.
Figs. 13 and 14.—*Unio aucklandicus* Gray: Holotype (two unmatched valves), BM. ×⅔.
Figs. 15–17.—*Unio lutulentus* Gould: Paratype, USNM Reg. No. 87847. ×⅔.

Plate 13

Hyridella (*Hyridella*) *miscoolensis* (Schepman): Figs. 1–3
Hyridella (*Protohyridella*) *glenelgensis* (Dennant): Figs. 4–6
Hyridella (*Nesonaia*) *guppyi guppyi* (Smith): Figs. 7–10
Hyridella (*Nesonaia*) *guppyi aipiana* (McMichael): Fig. 11

Figs. 1 and 2.—*Hyridella* (*H.*) *misoolensis* (Schepman): Lectotype, RNHL. ×⅔.
Fig. 3.—*Hyridella* (*H.*) *misoolensis* (Schepman): Seget. ×⅔.
Figs. 4–6.—*Unio glenelgensis* Dennant: Holotype, NMV. ×1⅓.
Fig. 7.—*Hyridella* (*N.*) *guppyi guppyi* (Smith): Aola, Guadalcanal; MCZ. ×⅔.
Fig. 8.—*Hyridella* (*N.*) *guppyi guppyi* (Smith): Fulakoro; MCZ. ×⅔.
Fig. 9.—*Hyridella* (*N.*) *guppyi guppyi* (Smith): Guadalcanal. ×1.
Fig. 10.—*Unio guppyi* Smith: Holotype, BM. ×⅔.
Fig. 11.—*Leiovirgus guppyi aipiana* McMichael: Holotype. ×1.

Plate 14

Hyridella (*Echyridella*) *menziesi* (Gray)

Figs. 1 and 2.—*Unio menziesi* Gray: Holotype, BM. ×⅔.
Fig. 3.—*Hyridella* (*E.*) *menziesi*, "*hochstetteri*" form: Lake Rotorua; MCZ. ×⅔.
Figs. 4–7.—*Unio lutulentus* Gould: Lectotype, USNM. ×⅔.
Fig. 8.—*Unio depauperata* Hutton: Lectotype, DMW. ×⅔.
Fig. 9.—"*Unio depauperata* Hutton": Topotype, DMW. ×⅔.
Fig. 10.—*Hyridella* (*E.*) *menziesi*, "*zelebori*" form: Albury Creek, N.Z.; MCZ. ×⅔.
Fig. 11.—*Hyridella* (*E.*) *menziesi*, "*zelebori/menziesi*" form: Te Papuni, N.Z.; MCZ. ×½.
Fig. 12.—*Diplodon menziesi acuta* Suter: Topotype, MCZ. ×⅔.

Plate 15

Cucumerunio novaehollandiae (Gray): Figs. 1–4
Cucumerunio websteri websteri (Simpson): Figs. 5–9

Figs. 1 and 2.—*Unio novaehollandiae* Gray: Syntypes, BM. ×⅔.
Figs. 3 and 4.—*Unio cucumoides* Lea: Holotype, AMNH. ×⅔.
Figs. 5–9.—*Diplodon websteri* Simpson: Lectotype, USNM. ×⅔.

Plate 16

Cucumerunio websteri delli, subsp. nov.: Figs. 1–5
Virgus beccarianus (Tapparone Canefri): Figs. 6–9
Haasodonta fannyae (Johnson): Figs. 10–12
Hyridella (*Hyridella*) *drapeta* (Iredale): Fig. 13

Figs. 1–3.—*Cucumerunio websteri delli*, subsp. nov.: Holotype, AM. ×⅔.
Fig. 4.—*Cucumerunio websteri delli*: Paratype, Henderson, N.Z.; MCZ. ×⅔.
Fig. 5.—*Cucumerunio websteri delli*: Paratype, type locality; MCZ. ×⅔.
Figs. 6–9.—*Unio beccarianus* Tapparone Canefri: Topotypes, AM. ×⅔.
Figs. 10–12.—*Haasodonta fannyae* (Johnson): Holotype, MCZ. ×⅔.
Fig. 13.—*Hyridella* (*H.*) *drapeta* (Iredale): Juvenile specimen, Waraba Creek, Caboolture, Qld., showing beak sculpture pattern; DPUQ. ×3½.

Plate 17

Hyridella (*Hyridella*) *australis* (Lamarck): Fig. 1
Velesunio ambiguus (Philippi): Figs. 2 and 3
Westralunio carteri Iredale: Figs. 4 and 5

Fig. 1.—*Hyridella* (*H.*) *australis* (Lamarck): Mitchell R., Bairnsdale, Vic., showing beak sculpture pattern. ×2.
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Fig. 3.—*Velesunio ambiguus* (Philippi): Longitudinal section, outer gill of female. ×100.
Fig. 4.—*Westralunio carteri* Iredale: Longitudinal section, inner gill of female, marsupial region. ×100.
Fig. 5.—*Westralunio carteri* Iredale: Longitudinal section, outer gill of female. ×100.

PLATE 18

Alathyria pertexta pertexta Iredale: Figs. 1 and 2
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Fig. 1.—*Alathyria pertexta pertexta* Iredale: Longitudinal section, inner gill of female, marsupial region. ×24.
Fig. 2.—*Alathyria pertexta pertexta* Iredale: Longitudinal section, outer gill of female. ×60.
Fig. 3.—*Hyridella* (*H.*) *narracanensis* (Cotton & Gabriel): Longitudinal section, inner gill of female, marsupial region. ×60.
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Fig. 6.—*Cucumerunio novaehollandiae* (Gray): Longitudinal section, inner gill of female, marsupial region. ×66.
Fig. 7.—*Cucumerunio novaehollandiae* (Gray): Longitudinal section, outer gill of female. ×100.

PLATE 19

Alathyria pertexta magnifica, subsp. nov.: Figs. 1 and 2
Haasodonta vanheurni, sp. nov.: Figs. 3 and 4

Fig. 1.—*Alathyria pertexta magnifica*, subsp. nov.: Holotype. ×⅔.
Fig. 2.—*Alathyria pertexta magnifica*, subsp. nov.: Paratype. ×⅔.
Figs. 3 and 4.—*Haasodonta vanheurni*, sp. nov.: Holotype. ×⅔.

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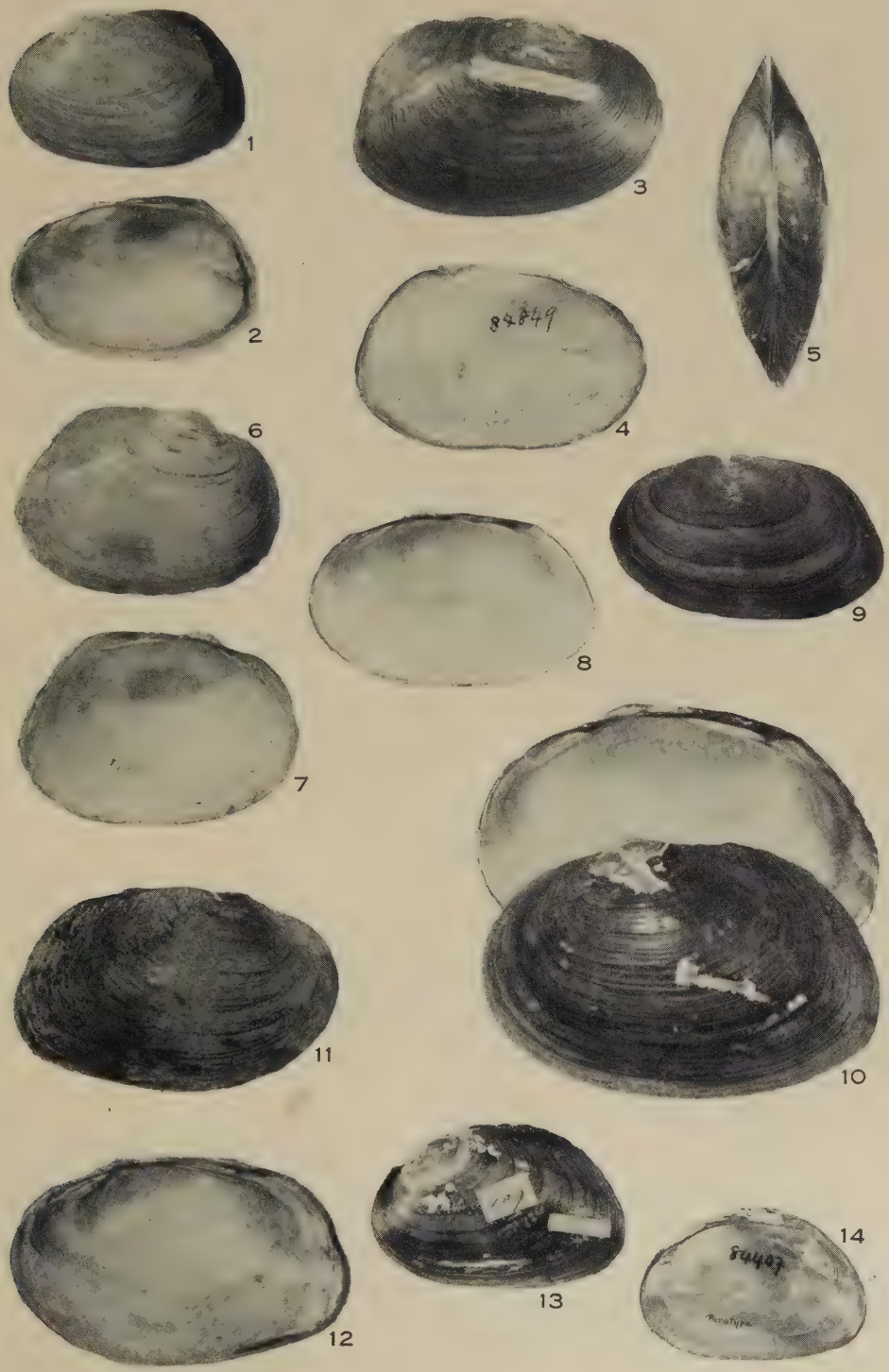
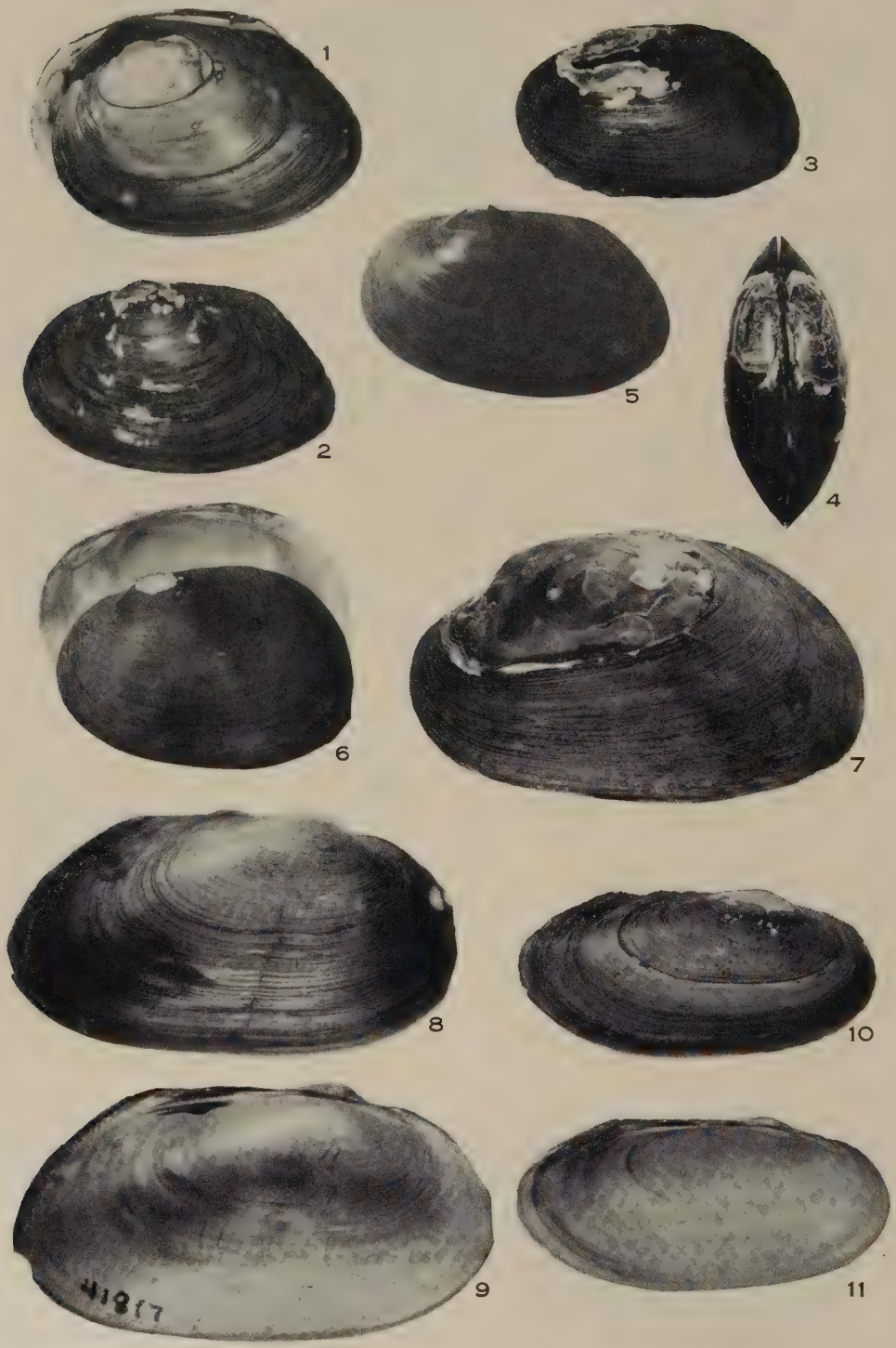
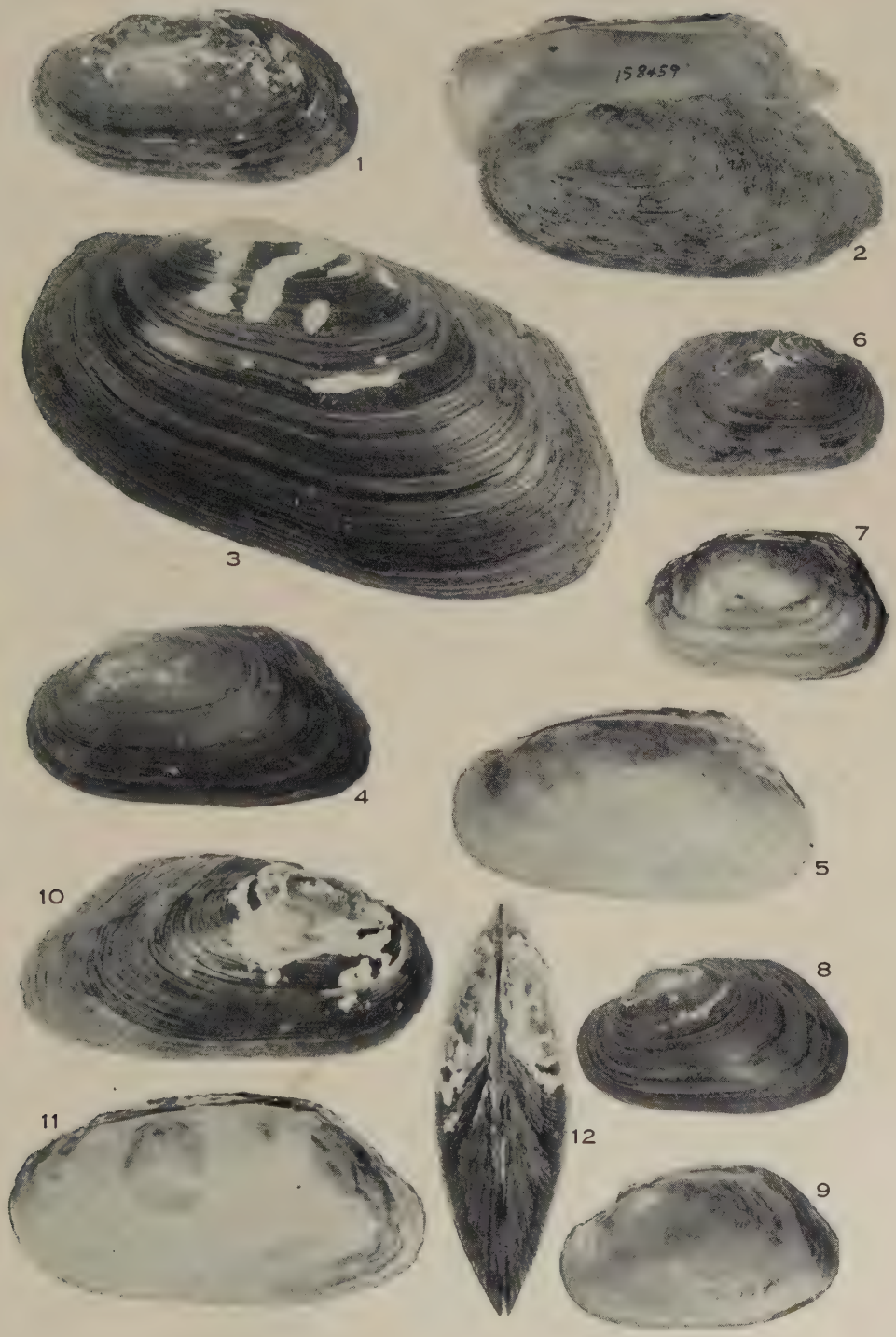
AUSTRALASIAN FRESHWATER MUSSELS



AUSTRALASIAN FRESHWATER MUSSELS



AUSTRALASIAN FRESHWATER MUSSELS



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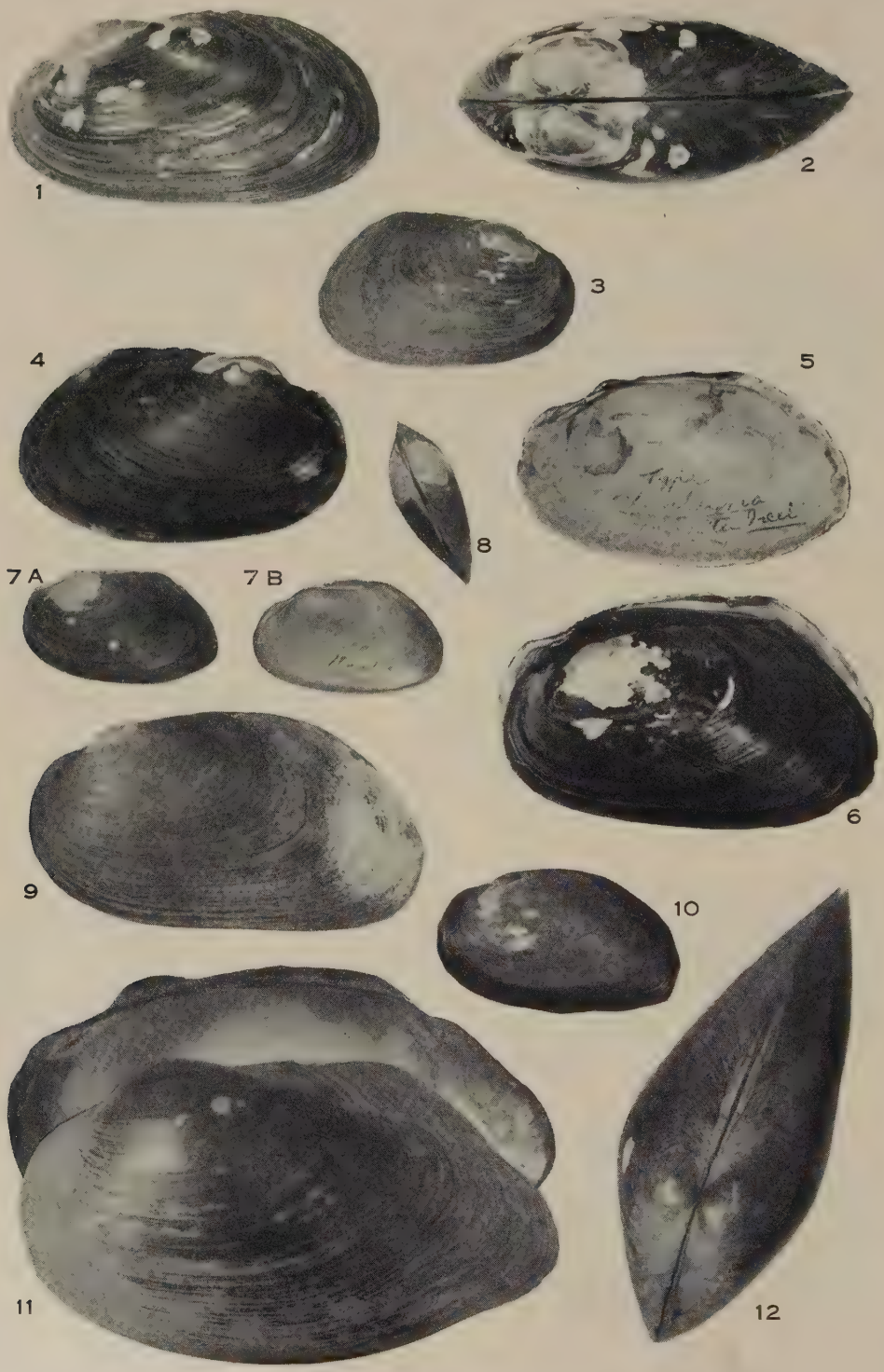

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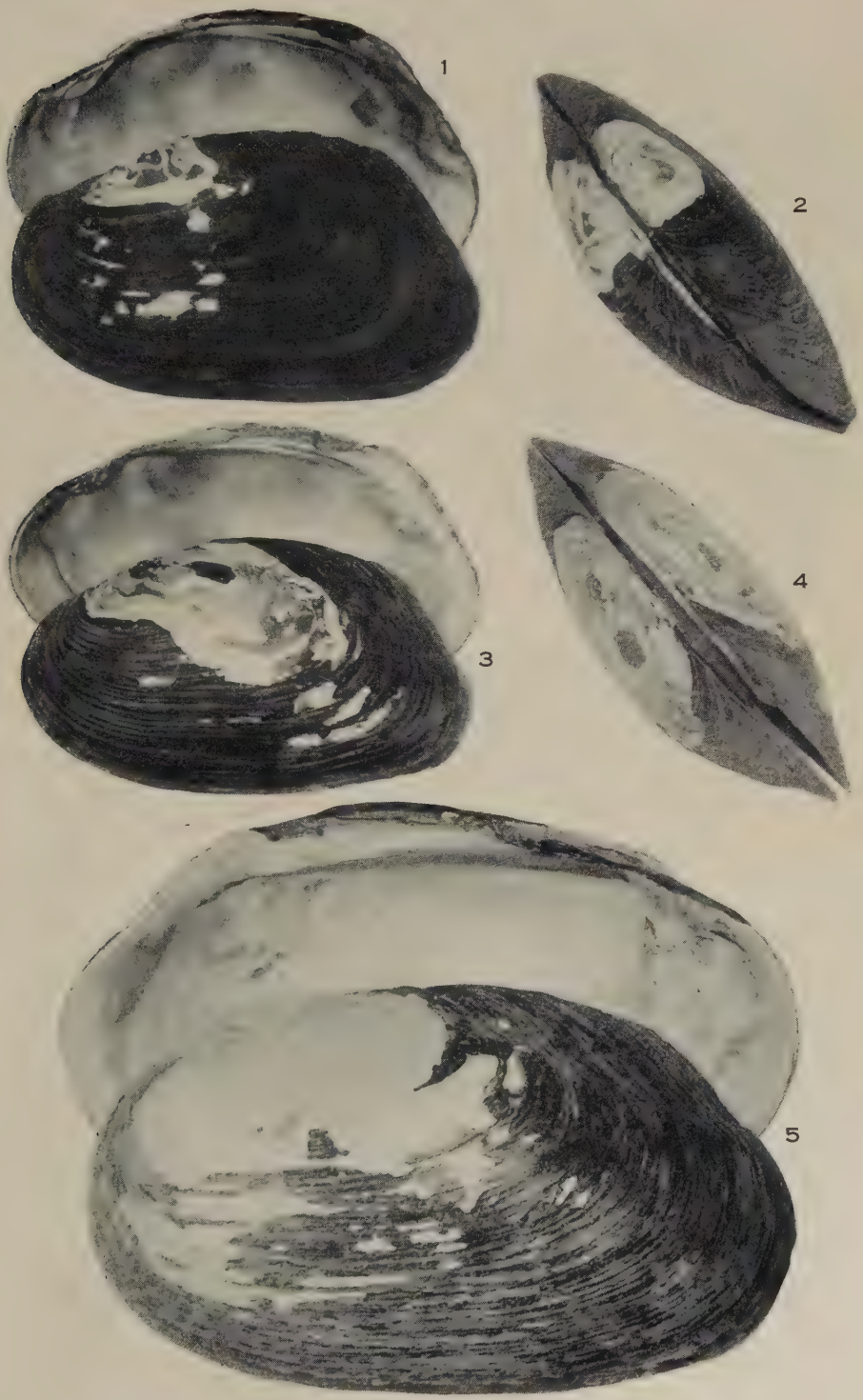

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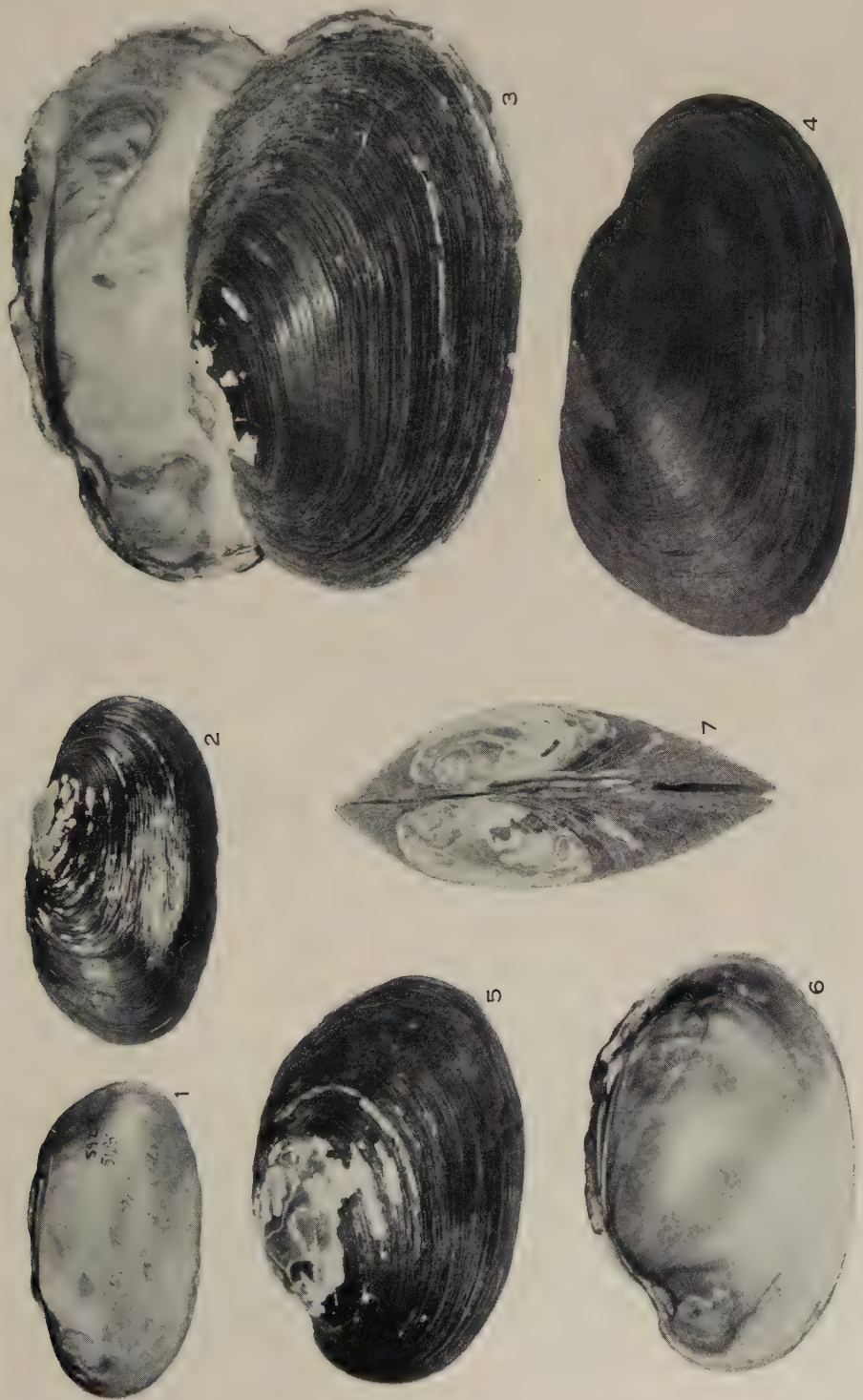

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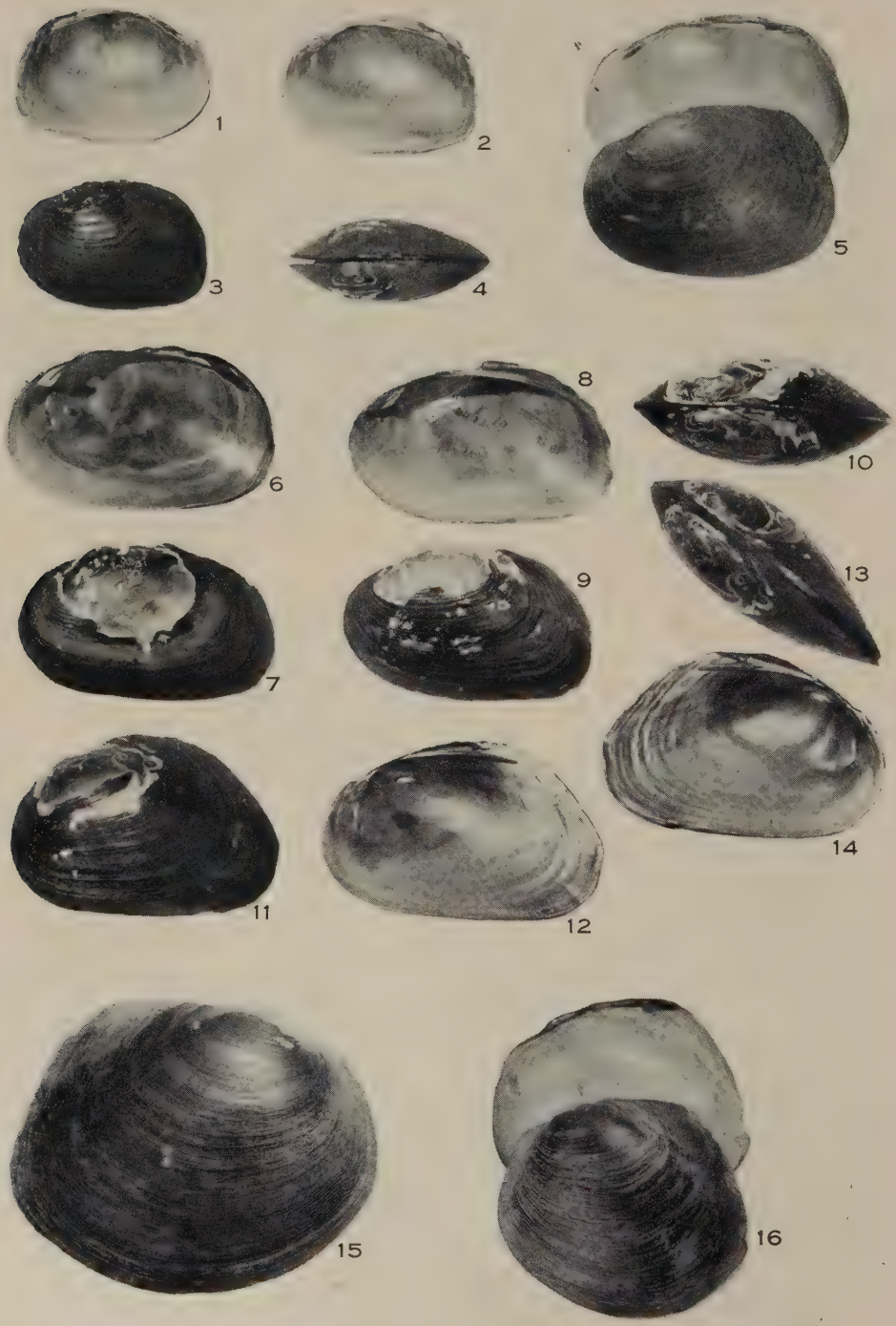

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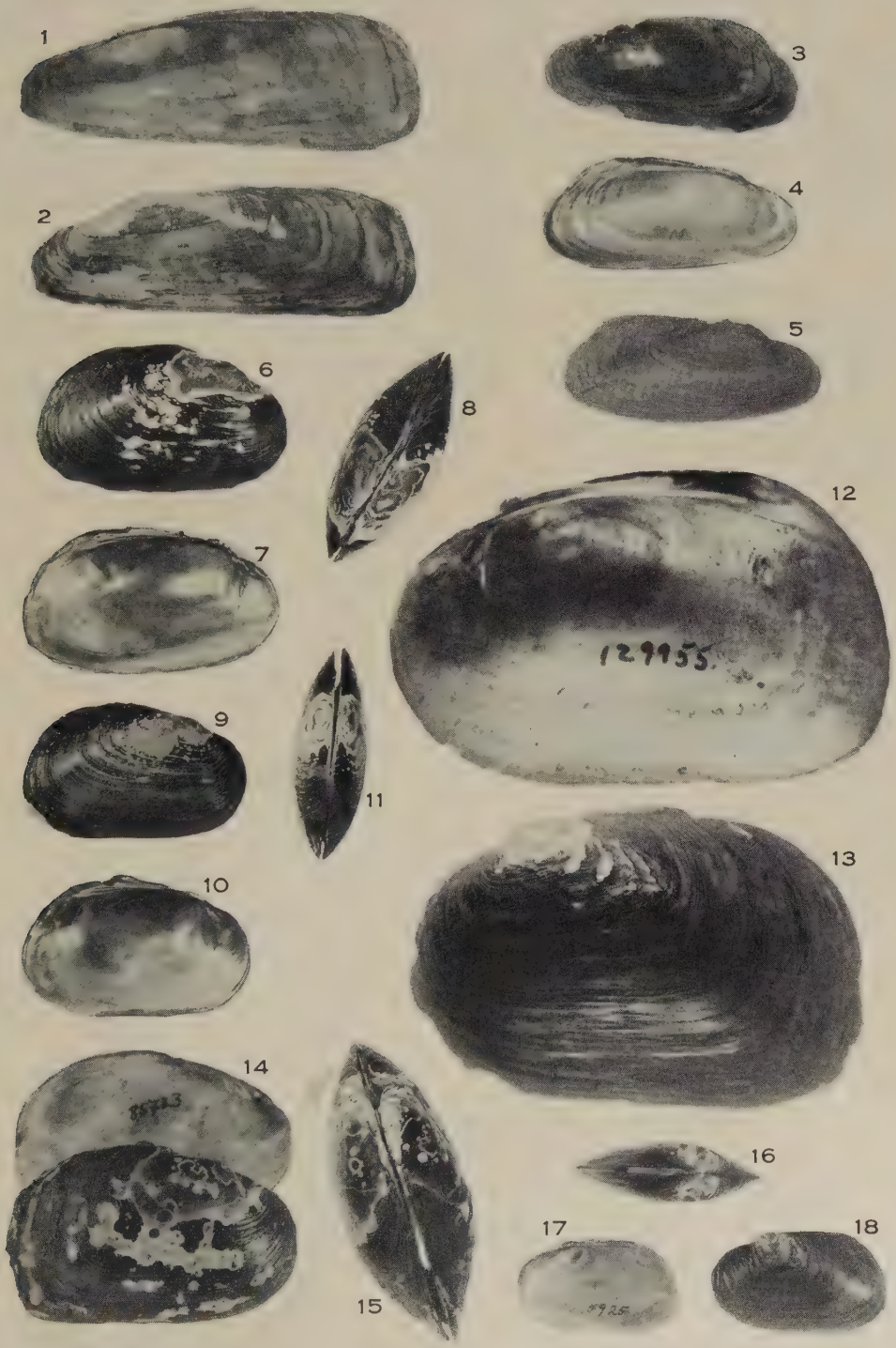

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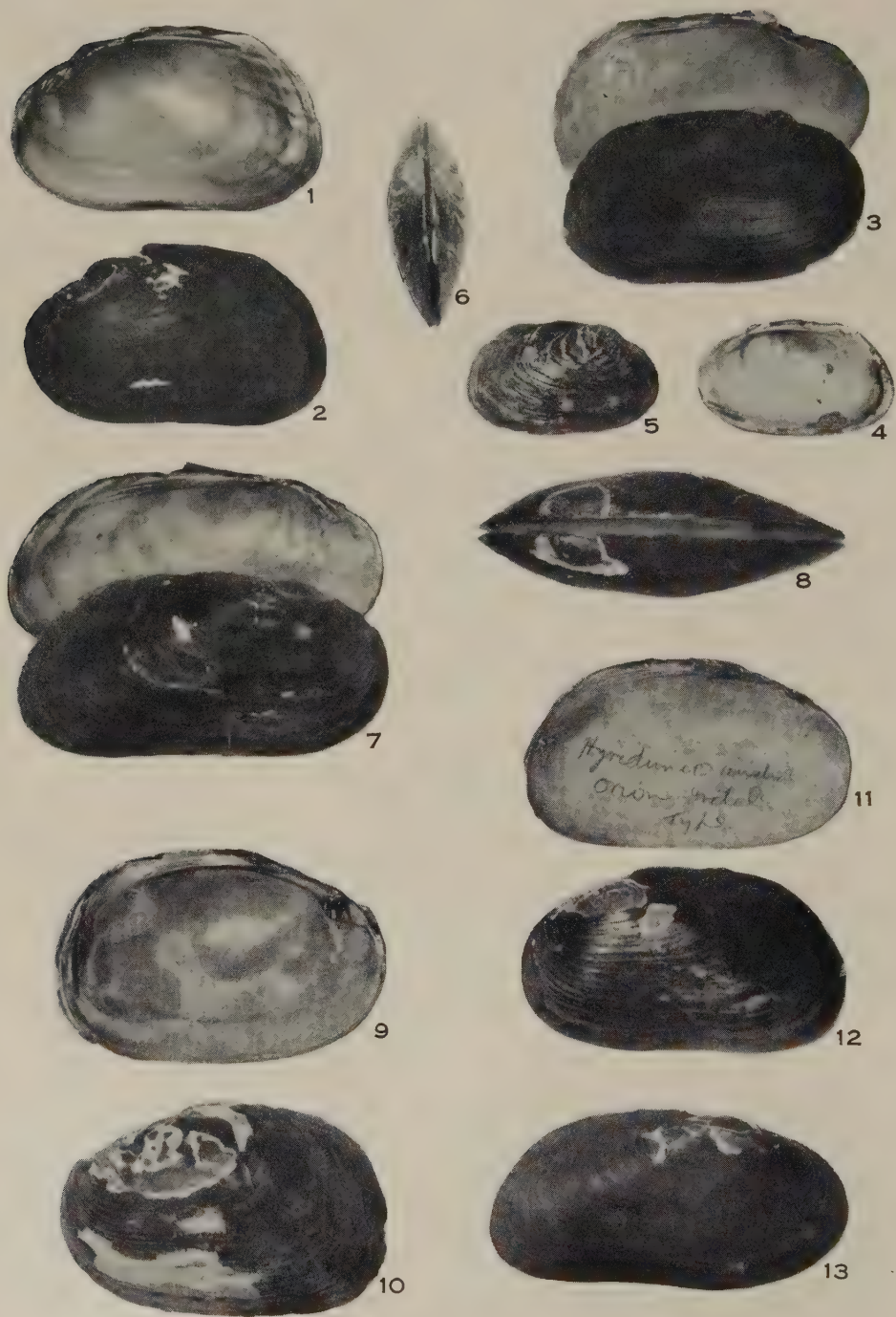

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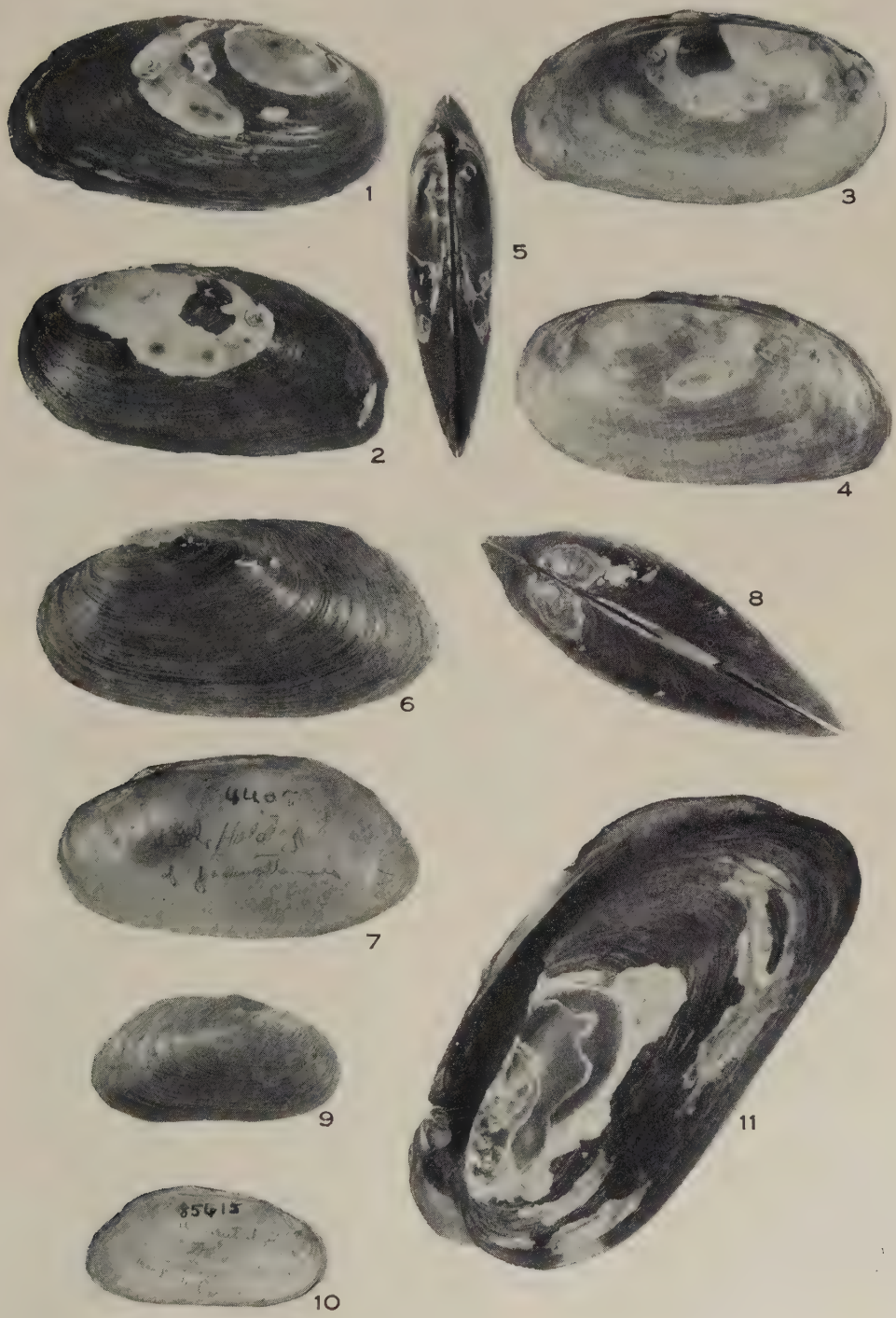

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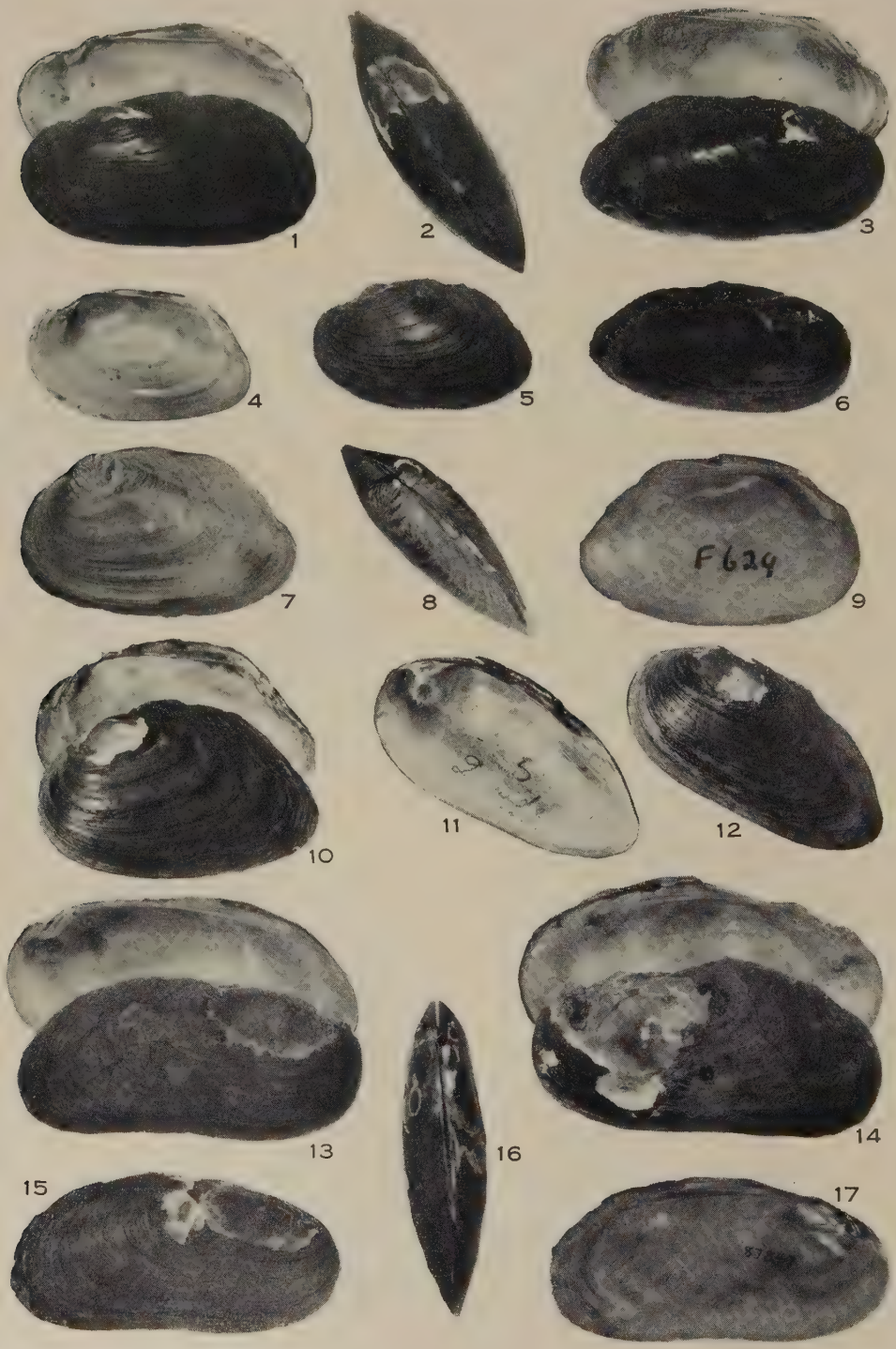

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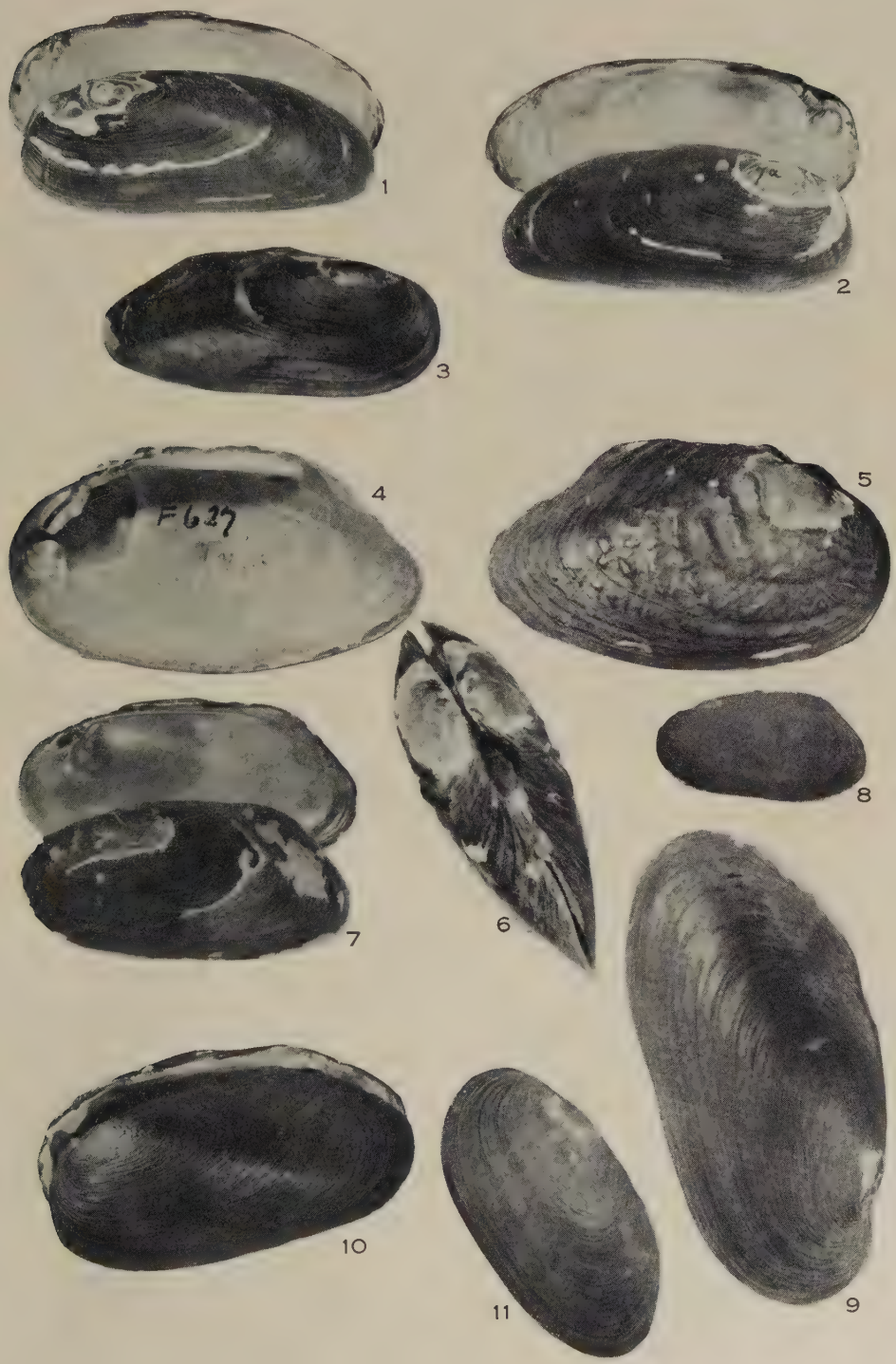

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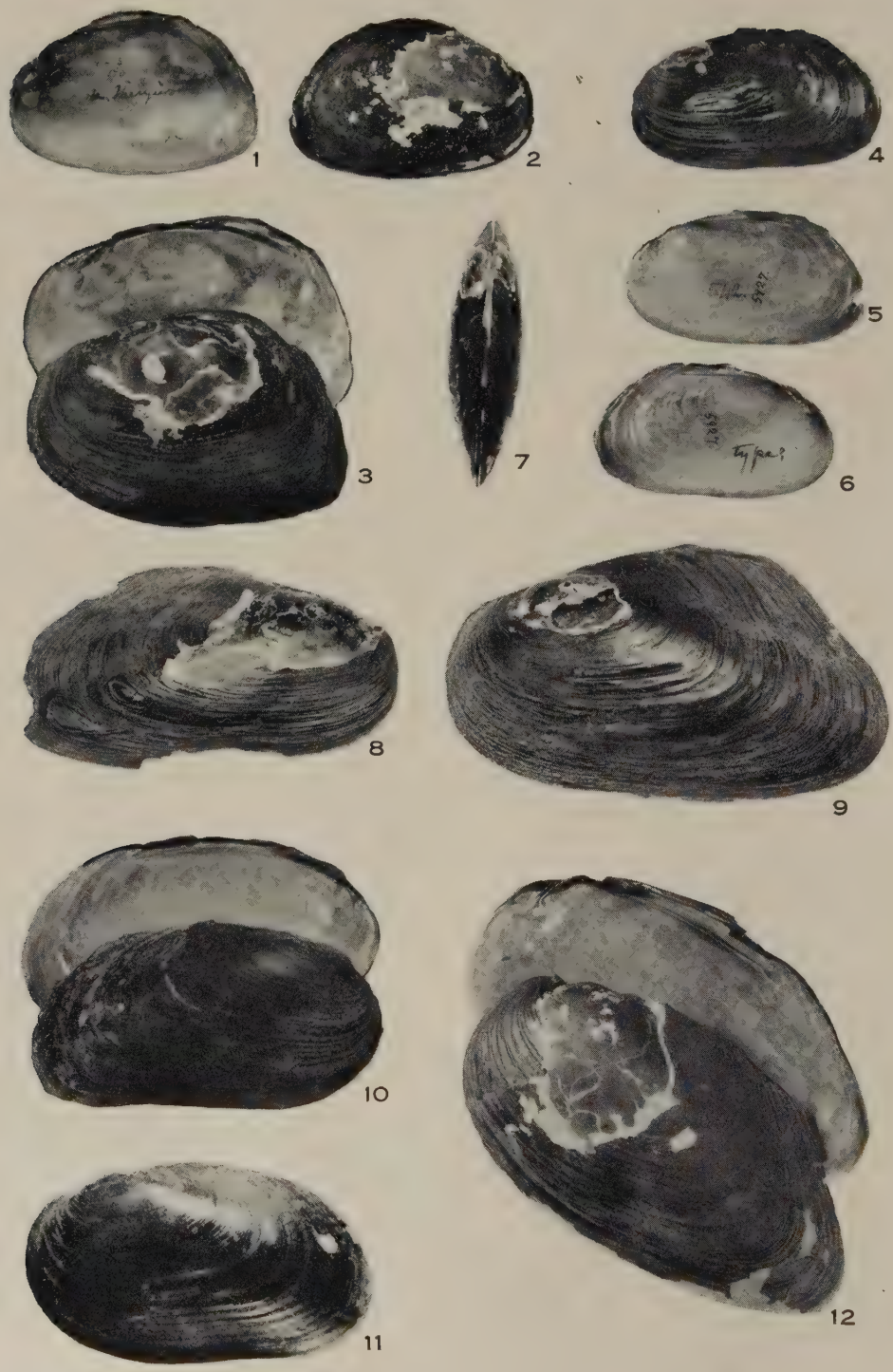

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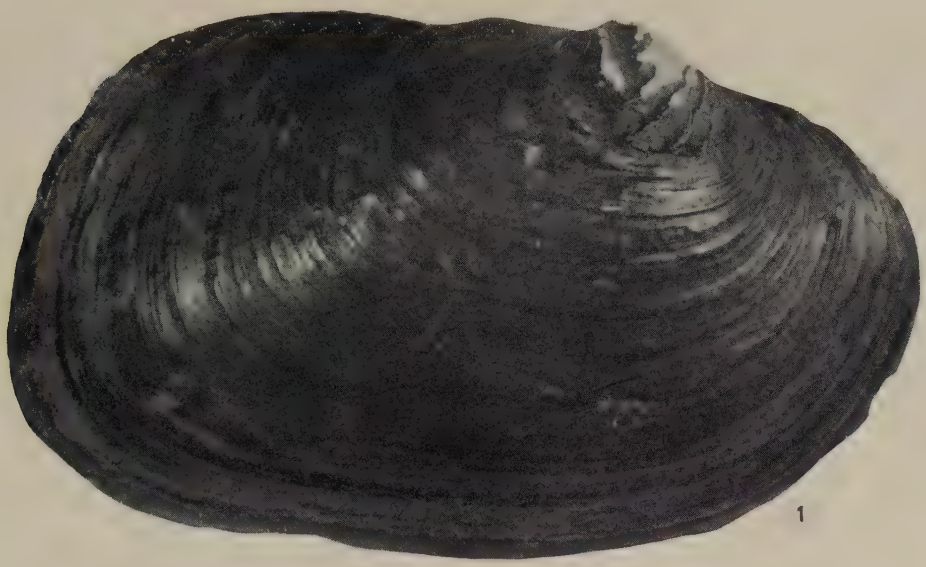

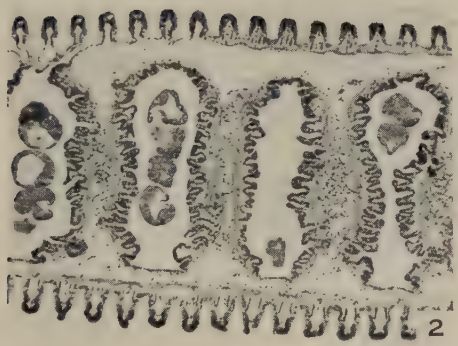

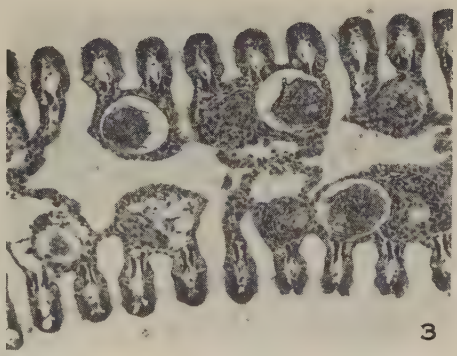

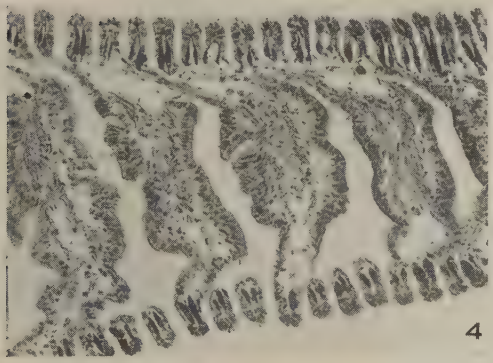

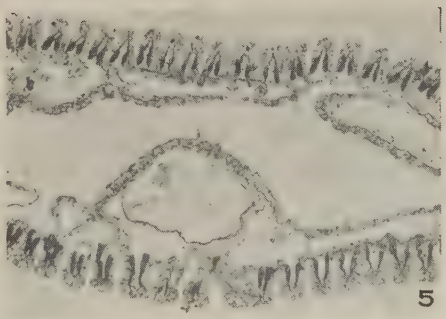

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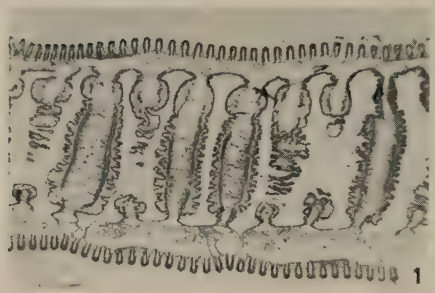
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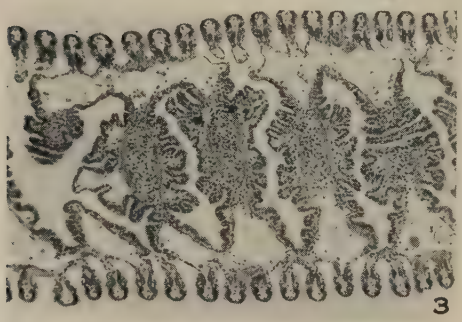
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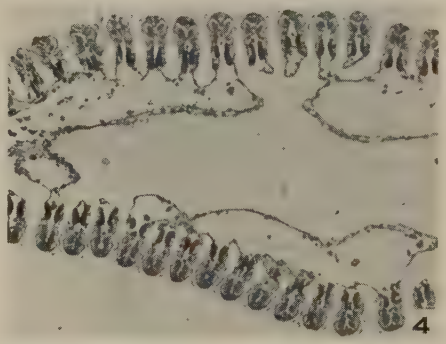
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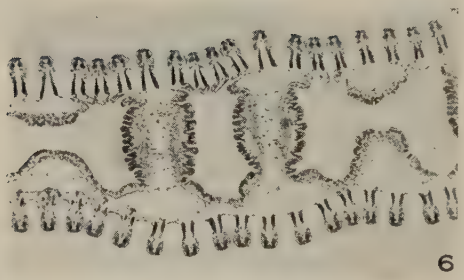
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AUSTRALASIAN FRESHWATER MUSSELS

REPRODUCTION IN AUSTRALIAN PEARL OYSTERS (LAMELLIBRANCHIA)

IV. PINCTADA MARGARITIFERA (LINNAEUS)

By D. J. Tranter*

[*Manuscript received July* 25, 1958]

Summary

The gonad of *Pinctada margaritifera* (L.) is similar to that of *P. albina* in appearance, development, and histological structure; minor differences are described and figured. Although the primary gonad may begin to develop within 12 months, complete and universal gonad maturity does not occur until the second year; compared with *P. albina*, then, the species is late-maturing.

At first maturity, less than 30 per cent. are females; in later seasons this shows a gradual rise to 50 per cent. Both protandric and protogynic sex-changes are occasionally seen in gonad sections and the evidence suggests that the process is a rapid one. It is therefore probable that sex-changes are common, and that the early increase in the percentage frequency of females is due to the more frequent occurrence of protandric change.

During 1956–57, major spawnings occurred in early January and late July, and lesser spawnings in other months. There were two distinct cycles: March to August, and September to February. It is considered, therefore, that breeding takes place predominantly in summer and winter, and may continue, at a reduced intensity, over the intermediate periods.

It is shown that the ripe oocyte becomes activated immediately prior to spawning. The germinal vesicle breaks down and meiosis proceeds to the metaphase of the first maturation division, at which stage there is a further arrestment. At fertilization, a second activation occurs and meiosis continues to completion. The maturation divisions and cleavage stages are described and figured.

I. Introduction

Pinctada margaritifera (Linnaeus) occurs throughout the coral areas of the Indo-Pacific, where it is known most commonly as the "blacklip pearl oyster". The species varies in form from area to area. Thus Jameson (1901) recognized six geographical varieties in *Pteria* (*Margaritifera*) *margaritifera*, as the species was then known, and designated the Australasian one, variety *typica*.

In common with the "silverlip pearl oyster" of the North Australia–Indonesia region, *P. maxima* (Jameson), the blacklip grows to a much larger size than do the other species in the genus. It may be distinguished from *P. maxima* by its greater convexity, shortness of hinge, and by its colour and markings (Jameson 1901; Hynd 1955; Tranter 1958*a*, Plate 1).

The species is fished commercially, particularly in the Polynesian region where pearl shell exports provide one of the major sources of income for the native peoples. As a result of its economic importance, the species has attracted the attention of many biologists. Observations have been recorded from French Oceania (Seurat

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1904*a*, 1904*b*; Hervé 1934; Ranson 1952, 1955), the Great Barrier Reef (Nicholls 1931), the Philippines (Talavera and Faustino 1931), Hawaii (Galtsoff 1933), Panama (Galtsoff 1950), and the Red Sea (Crossland 1957). There are varied opinions concerning the breeding season and sexuality of the species. It is with these aspects that the present work is mainly concerned.

It is necessary here to clarify the taxonomic position of the pearl oysters from Hawaii and Panama dealt with by Galtsoff. Jameson (1901) examined specimens from both localities, and from Mazatlan (Gulf of California). He considered that these could definitely be linked to the *typica* variety of the species *margaritifera* and listed them as variety *mazatlanica*. However, Bartsch (1931) renamed the Hawaiian pearl oyster, *P. galtsoffi*. Galtsoff (1933) followed Bartsch for Hawaiian material and revived *mazatlanica* Hanley, 1855 for the Panama pearl oyster (Galtsoff 1950). However, his illustrations of the two types, together with his comments on their habitat, leave little doubt that both belong to *P. margaritifera* (L.) and possibly both to Jameson's variety *mazatlanica*.

II. Materials and Methods

The material on which this study is based is from the Torres Strait area, and consists of: (1) irregular samples taken from a variety of localities over a period of several years, and (2) regular monthly samples from a group of 300 oysters collected on Dove and Bet Reefs in June 1956. The location of these areas is shown in Figure 1.

The latter group was placed in an inflatable swimming pool on board the Lighthouse Service Vessel *Cape Leeuwin*, provided with running sea-water, and transported to the Thursday Island laboratory; they were 2 days in transit. On arrival, they were placed in wire-netting cages and suspended from a bamboo raft anchored in shallow water near the laboratory. The oysters showed no ill-effects from their transfer, and new growth processes were soon laid down. In July 1956, the younger ones were culled out and their gonads fixed. From August 1956 to August 1957 the remainder were sampled at monthly intervals (20 per sample) and their gonads also fixed. The fixed material was later sectioned, stained, and examined in detail. Gonads were classified in two ways:

(i) *Macroscopic Appearance.*—As in earlier papers (Tranter 1958*a*, 1958*c*) the "fullness" of the gonad was indicated as follows: 0, empty; 1, partly full; 2, nearly full; 3, full. These correspond to the stages "empty", "immature", "nearly mature", and "mature" which Nicholls (1931) adopted for the same species.

(ii) *Gametogenic Activity.*—As in *P. albina* (Lamarck), histological criteria were used to assess the state of gametogenic activity of each gonad, eight stages being recognized for each sex and one for the undifferentiated gonad (Tranter 1958*c*). The method of classification was modified somewhat for *P. margaritifera* because of the rather different pattern of gonad regression; these modifications are listed in Section VI.

As with other pearl oysters, there are no growth lines in this species which may be used for age determination. Young oysters may, however, be distinguished from old ones by their vigorous growth processes, fresh colouration, freedom from shell infestation and erosion, and by their shell dimensions. In this study, shell

measurements are used to estimate age. Records were kept of weight, heel depth, and dorsoventral length. Of these, heel depth shows the most consistent increase throughout the life of the oyster (as judged by other criteria) and it is used later as a measure of age at first maturity and as a record of the changing sex ratio.

Fig. 1.—Map of eastern Torres Strait area showing localities mentioned in text.

III. Gonad Morphology and Development

The gonad of *P. margaritifera* is similar in most respects to that of *P. albina* (Tranter 1958*a*). There is, however, a greater proliferation of gonad follicles in the area between byssal gland and gut loop. Oysters may be sexed on gonad colour with an error of less than 5 per cent.—the male gonad is lighter than that of the female which is usually yellow or creamy yellow. Nicholls (1931) observed the same gonad colouration in the Low Isles population. The testes and ovaries of Red Sea material show a similar difference in colour, although both are somewhat paler (Crossland 1957). However, Hervé (1934) and Ranson (1952) describe the ovary of the Tuamotu blacklip as pinkish.

Development of the gonad follows the pattern described by Seurat (1904*b*) and Tranter (1958*a*). During primary gonad differentiation the fine follicular network is more conspicuous than in *P. albina*, and the primary follicles are only partly

germinal. As in that species, there is a seasonal inactivity of the gonad not readily distinguishable from immaturity.

IV. Gonad Histology and Germ Cell Development

The pattern of gametogenesis in *P. margaritifera* closely resembles that in *P. albina* (Tranter 1958*a*, 1958*b*). The primary follicles and their associated stem cells are laid down in the same way; the gametogenic cycle pursues a similar course and with comparable velocity; corresponding germ-cell stages are of similar appearance and dimensions, and are distributed in a like fashion, with respect to each other and to the follicle wall. Nevertheless there are the following differences:

(i) The primary follicles, which initiate the spread of the gonad throughout the connective tissue areas in primary gonad development, become partly differentiated as gonoducts. As in *P. albina*, the urogenital pore is heavily ciliated (Plate 2, Fig. 1); however, this ciliation, although greatly reduced, extends into the primary gonad follicles along the wall closest the surface (Plate 2, Fig. 2). Distal to the urogenital pore the ciliation gradually disappears, and the follicles are completely germinal.

(ii) Spawning is universally more thorough, with the following consequences: there are fewer residual products, and therefore phagocytosis plays a lesser role in gonad regression than in *P. albina*; there is less overlapping of phases within the gonad follicles, regression usually becoming complete before the commencement of the next developmental cycle; bisexual gonads are less common.

(iii) Activation of the ripe ovarian oocyte. In *P. albina* (Tranter 1958*b*), meiosis in the female gonad was never observed to proceed beyond prophase, a stage reached early in oocyte growth and maintained at this level till spawning. The ripest ovarian oocytes had intact germinal vesicles, and since these could not be broken down artificially by contact with sea-water or ripe spermatozoa, it was concluded that an activating stimulus occurs immediately after the egg leaves the follicle. In *P. margaritifera*, however, sections across gonad follicles during spawning (Plate 1, Fig. 6; Plate 2, Figs. 3 and 4) show that ripe oocytes become activated while still within the follicle.

(iv) Yolk nuclei within the oocyte. Disposed at random throughout the cytoplasm of a number of advanced oocytes are large, ring-like structures up to 8 μ in diameter with a thickness of about 1 μ. Some are only faintly visible, but the majority are strongly basophilic and extremely conspicuous (Plate 2, Figs. 5 and 6). In section, many appear crescent-shaped. These have been identified as yolk nuclei.

(v) The occurrence of late stage primary and secondary spermatocytes. In a few gonads, primary spermatocytes were observed in late diplotene configuration. This, and the following stage (metaphase), are usually of short duration in spermatogenesis, so that the observation of their presence in these cases may have been due more to chance than to a slower development rate at this stage. The cells are large and round (5–6 μ in diameter) with an intact nuclear membrane. There is no observablecytoplasm. Clearly evident, and disposed evenly throughout the nucleus, are a number of chromosome pairs with terminalized chiasmata (Plate 2, Fig. 7).

Secondary spermatocytes in late prophase were commonly observed in this species though seldom in *P. albina*. They are small, round (2·5–3 μ in diameter), densely staining cells without visible cytoplasm. The nuclear rim is particularly basophilic. They lie in masses just outside the central core of spermatids and spermatozoa (Plate 2, Fig. 8).

(vi) The occasional presence of unusual intrafollicular phagocytes. These are either round or oval (mean diameter 6–7 μ) with a nucleus that varies in form from round (diameter 2·5 μ), to bi-lobed or double, and is densely reticulate (Plate 2, Fig. 9). Since the cytoplasm is hyaline and, occasionally, denser chromatin bars may be seen within the nucleus, it is considered that these phagocytes are related to the cell type B of *P. albina* (Tranter 1958*b*).

V. Nuclear Maturation and Early Cleavage

On two occasions (November 1956 and August 1957) the monthly oyster samples contained a number of individuals which had recently ingested a quantity of spawned eggs. These could be seen in sections across the stomach and digestive diverticula adjacent to the gonad. Such a variety of fertilization and cleavage stages were represented that it was possible to trace practically the whole history of the egg to the gastrula stage.

Wada (1942, 1953) observed the fertilization and development of *P. maxima* eggs; however, the *P. margaritifera* sections show details of nuclear maturation and cleavage not hitherto recorded for pearl oysters; therefore they are here described and figured.

Activation of the ripe ovarian oocyte is evidenced by profound structural changes, the most obvious of which are the breakdown and disappearance of the large clear germinal vesicle (Plate 1, Fig. 6) and the resumption of meiosis. The chromosomes, thus liberated, migrate to the future animal pole where a spindle is being formed. This is the prometaphase period (White 1950, p. 61). When the chromosomes become arranged in metaphase configuration upon the spindle (Plate 2, Figs. 3 and 4) meiosis is once more arrested. The egg is spawned at this stage, and there is no further change in structure or meiotic configuration until fertilization takes place.

When this occurs, the maternal chromosomes rapidly pass through the anaphase and telophase of the first maturation division giving rise to the first polar body (Plate 3, Fig. 1). This is followed soon after by the second maturation division, the second polar body being formed immediately beneath the first, which now projects beyond the cytoplasm (Plate 3, Figs. 2 and 3). The vitelline membrane is lifted away from the cytoplasm at this point to form a conical protuberance on the otherwise spherical egg.

The sperm-head, during its advance through the cytoplasm of the egg (Plate 3, Figs. 1–3), increases greatly in size, and its chromatin material becomes dispersed throughout the enlarged nuclear area. It is now known as the male pronucleus and, by the time the female pronucleus is formed, has become a large, round (6–10 μ in diameter), clear body containing finely divided chromatin. The female pronucleus forms near the animal pole from the telophase of the first maturation division

(Plate 3, Fig. 2). It is slightly smaller than the male pronucleus and imperfectly spherical (Plate 3, Figs. 2 and 3). The two pronuclei move toward a common position in the cytoplasm where they eventually fuse (Plate 3, Fig. 4). This position, and the respective paths which the pronuclei take to arrive there, vary from case to case. As the pronuclei fuse, the area at the vegetal pole assumes a more transparent appearance and begins to protrude from the main cell mass (Plate 3, Fig. 4). This gives rise to a "polar lobe" (Plate 3, Figs. 5 and 6) which is excluded from the first cleavage division.

The breakdown of the zygote nucleus and the formation of the first cleavage spindle take place rapidly, and these processes were not represented in the sections. The first cleavage is along the polar axis so that the polar bodies come to lie in the cleavage furrow (Plate 3, Fig. 5); the resulting body is of a trefoil form (Plate 3, Fig. 6). This could be easily mistaken for a three-cell stage, but there is, of course, no nucleus within the polar lobe.

The two-cell stage consists of a micromere and a macromere, the latter being the result of fusion between one of the first daughter cells and the first polar lobe (Plate 3, Fig. 7). The nuclei are clear, round bodies, centrally placed. The micromere divides normally into two daughter micromeres, but the macromere, as at the first division, gives rise to two micromeres and a polar lobe (Plate 3, Fig. 8). The four-cell stage (Plate 3, Figs. 9 and 10) is formed when this second polar lobe fuses with one of the latter micromeres. The following divisions (Plate 3, Fig. 11) are normal, resulting in an eight-cell stage. The gastrula (Plate 3, Fig. 12) is formed by epiboly.

VI. Breeding Season

Gonads were classified on histological criteria as follows (*M*, male; *F*, female; d_1–d_5, stages of gonad development; r_1–r_3, stages of gonad regression; *i*, inactive):

Md_1	Predominantly stem cells and spermatogonia; few spermatocytes.
Md_2	Predominantly spermatogonia and spermatocytes; few spermatids or sperm.
Md_3	Space occupied by spermatocytes now equalled by that of sperm (and spermatids); few tailed sperm; follicles still small.
Md_4	Follicles large; broad band of spermatocytes; spermatozoa often tailed.
Md_5	Predominantly sperm, majority tailed; spermatocytes restricted to narrow peripheral band.
Mr_1	As for Md_4 or Md_5 except that many follicles partly emptied, some completely.
Mr_2	Spawning well advanced; peripheral cells now conspicuous.
Mr_3	Spawning practically complete; few germ cells remain.
i	As for *P. albina* (Tranter 1958*b*).
Fd_1–Fd_5	As for *P. albina*.
Fr_1	Many follicles partly or completely empty.
Fr_2–Fr_3	As for Mr_2, Mr_3.

The stages d_4, d_5, and r_3 are illustrated for both sexes in Plate 1, Figures 1–6. The monthly diagnoses of gonad activity are summarized in Table 1, following the method adopted for *P. albina* (Tranter 1958*c*).

The August 1956 sample contained a number of gonads with residual products, suggesting that there had been a recent spawning. The remaining gonads were, in the main, fairly ripe (d_4 and d_5). The number of ripe gonads in the September sample was even higher, indicating that the August–September period was one of active gametogenesis.

TABLE 1

HISTOLOGICAL CLASSIFICATION OF GAMETOGENIC ACTIVITY IN REGULAR MONTHLY SAMPLES OF ADULT OYSTERS

M, male; *F*, female: *d*, development: *r*, regression; *i*, inactive. The subscripts 1–5 of *d* indicate the stages of gonad development, and 1–3 of *r* the stages of gonad regression. For the purpose of comparing the general level of development and regression in the various monthly samples, the subscripts are treated as units of gonad development and regression respectively

Date	Numbers of Individuals in Each Stage									Bisexual	Totals		
	i	d_1	d_2	d_3	d_4	d_5	r_1	r_2	r_3		i	d	r
15.viii.56			1		6	6	5		2			56	11
17. ix.56					8	11				Md_4Fr_2†		91	2
15. x.56					16		3	1				64	5
15. xi.56*					4	5	9	2				41	13
17. xii.56					10	5	4	1				65	6
18. i.57	2					1	4	8	5		2	5	35
21. ii.57	4					1	3	3	9		4	5	36
25. iii.57			1	2	14	2	1					74	1
23. iv.57						19		1				95	2
21. v.57					2	9	7	1	1			53	12
18. vi.57						16	4					80	4
15. vii.57						15	3	2				75	7
14.viii.57	1					3	5	8	2	Fd_5Mr_1†	1	20	28

*Spawned in laboratory. †Bisexual gonad.

During October, there was limited spawning. This is indicated not only by the presence of individuals with "residual gonads" but also by the lowered developmental level of the remainder. These are individuals which have spawned and are re-ripening without follicle regression. Such redevelopment may be clearly seen in sections: in the male there is a broad band of spermatocytes recently formed, and in the females there is a new crop of oocytes.

The November sample spawned in the laboratory, and since this spawning may have been caused by handling, it is not considered here, except to illustrate that, at this time, the gonads were ripe and capable of spawning.

The December sample was riper than that of October. Between the sampling dates for December and January, there was a sudden major spawning. The period

mid January to mid February was one of recovery; partially spent gonads were emptied completely, and occasional gonads regressed to a completely undifferentiated state.

Late February and March was a period of vigorous gonad redevelopment similar to that of the previous September. By mid April, practically all individuals were fully ripe. There was a little spawning during the succeeding months but, in general, the level of gonad ripeness was maintained till mid July. During late July and August,

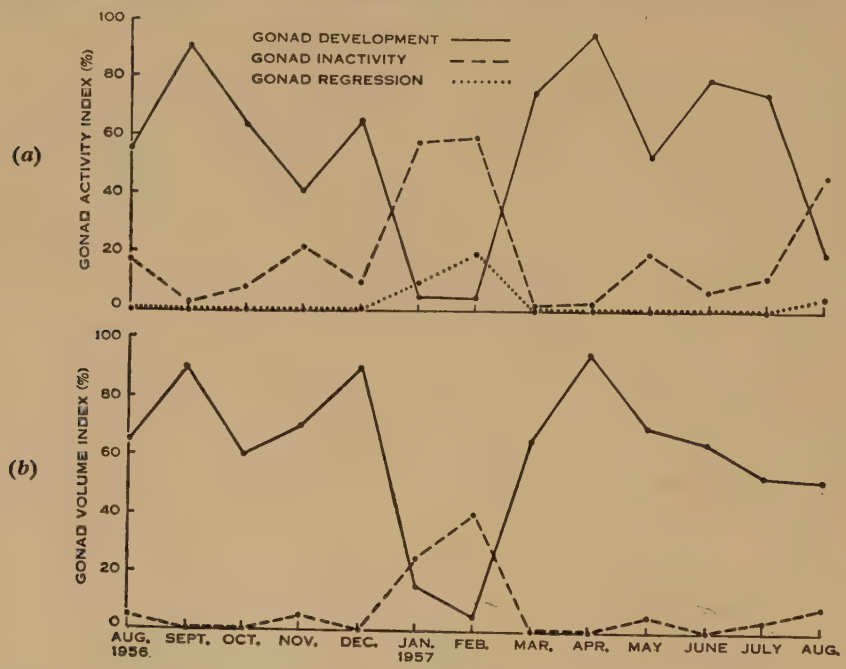

Fig. 2.—Breeding season of *P. margaritifera* as indicated by trends in:
(*a*) Gametogenic activity: the Gonad Activity Index for each monthly sample represents the general extent of development, regression, and inactivity of the germ cells relative to the maximal value (100 per cent.) for each of these three conditions.
(*b*) Macroscopic gonad appearance: the Gonad Volume Index represents the percentage frequencies of full and empty gonads in each monthly sample.

there was another major spawning. The August sample had ingested a number of their own spawn and these were clearly seen, in sections, lodged in the stomach and digestive diverticula. They included many fertilized eggs and cleavage stages.

These trends may be illustrated graphically by the following means: since d_5 and r_3 represent the individual maxima (limits) of gonad development and gonad regression, then for a sample of 20, the sample maxima will be 20 d_5 and 20 r_3, respectively. Now, if the subscripts 1–5 of d and 1–3 of r are regarded as units of gonad development and gonad regression respectively, then the sample maxima are equivalent respectively to 100 d-units and 60 r-units. It is now possible, by summing the d and the r subscripts in each sample, and expressing these totals as percentages of the maximum, to give a value to the general extent of gonad development and gonad regression in each sample.

These percentage values are plotted graphically in Figure 2(*a*) and the curves compared with those based on macroscopic observation (Fig. 2(*b*)). It has not been necessary to smooth by the moving average method as was the case with the *P. albina*

TABLE 2

BIANNUAL BREEDING BEHAVIOUR

Cycle (*a*)	Cycle (*b*)	Gonad Activity
September	March	Vigorous gametogenic activity; gonads ripen
October	April	Limited spawning; but gonads rapidly fill again
November	May	
December	June	
January	July	Major spawning (early January, late July)
February	August	Period of recovery; gonads continue to empty; some regress completely; others begin to redifferentiate

data (Tranter 1958*c*). Seasonal trends are clearly shown: there are two distinct cycles—March to August and September to February. The general sequence of events within each cycle is summarized in Table 2.

TABLE 3

MACROSCOPIC OBSERVATIONS ON THE SEX AND GONAD STATE OF VARIOUS SAMPLES TAKEN AT IRREGULAR INTERVALS

Locality	Date	Sample Size	Gonad Stage (Frequency, %)				Sex	
			3	2	1	0	♂	♀
Dungeness I.	19. vii.53	18	11	78	11	0	77	23
Dungeness I.	17.viii.53	33	30	45	25	0	39	61
Stephen I.	20.viii.53	30	43	40	17	0	43	57
Nepean I.	23.viii.53	5	60	20	20	0	40	60
Calico Reef (Darnley)	25.viii.53	7	43	43	14	0	57	43
Darnley I.	27.viii.53	9	33	44	23	0	66	34
Darnley I.	4. ix.53	13	69	16	0	15	64	36
Yam I.	22. v.54	10	90	10	0	0	40	60
Dungeness I.	20. vi.54	18	44	56	0	0	50	50
Stephen I.	13. vii.54	51	82	14	0	4	55	45
Dungeness I.	16. vii.54	55	98	0	0	2	61	39
Dungeness I.	17. ix.54	81	90	10	0	0	64	36
Stephen I.	14. ii.55	25	28	40	0	32	53	47

In addition to the evidence presented above, observations have been made, also, on the gonad condition of samples taken at irregular intervals from a variety of localities in the Torres Strait area (for map, see Fig. 1); these are listed in Table 3.

This evidence, although of limited significance, is in agreement with that already presented.

Nicholls (1931) concluded that the species spawns in November and May. Between September 17, 1928, and May 27, 1929, he observed the gonad condition of 160 oysters at Low Isles (15°S.), and also of a number at Murray Island on May 10 and 12, 1929. Observations at Low Isles were made twice a month, and the samples were fairly regular until February, after which the numbers examined began to decrease.

The observations clearly show that there was, indeed, a major spawning in November. However, the evidence that there was another major spawning in May is less convincing. This is as follows: on March 11 gonads were observed to be filling, "from then onwards the gonads filled gradually and it was expected that by the end of April they would be fully mature" (the specimens examined on April 11 consisted

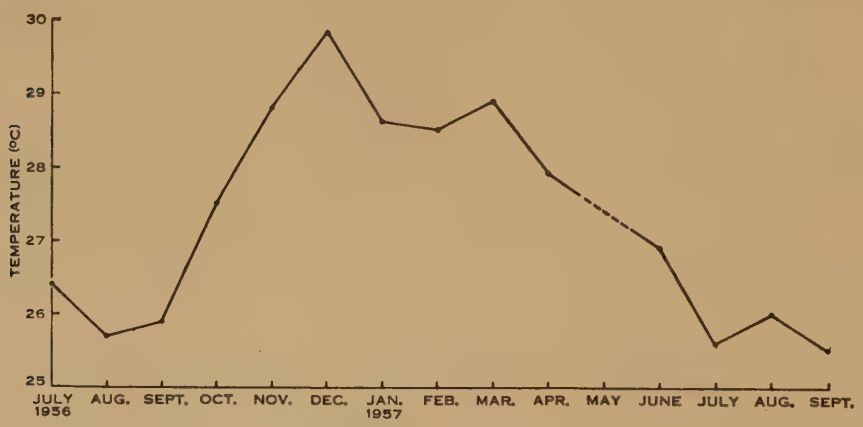

Fig. 3.—Mean monthly sea temperatures at Thursday I. during the main observational period.

of two with empty gonads, and nine with "immature" (filling) gonads); on May 10, three gonads were examined—one was "immature," one "nearly mature" and one "mature"; on May 27 two were examined, both of which were spent. This has been taken to mean that spawning took place between May 10 and May 27, and the following evidence is offered in support: on May 10, at Murray Island, "specimens" (number unknown) were found to be mature; on May 12, six specimens were examined, two of which were spent and the rest "ready to spawn at any moment"; on May 27, at Low Isles, a few young individuals with very thin shells were found, and it was presumed that these had arisen from a spawning earlier in the month.

It is impossible to tell from such limited evidence whether or not there was a major spawning at this time. In the first place, it is unlikely that the spat found could be attributed to the spawning observed, if indeed they were the same species (identification is very difficult at this stage); in the second place the numbers examined were too small—the evidence consists, in fact, of four oysters with spent gonads, two at Murray Island on May 12 and two at Low Isles on May 27.

Since Nicholls's observations began in September 1928 and ceased in May 1929, it is also impossible to tell whether there was a major spawning in August, as in the Dove and Bet Reef material. It is possible that the May spawning of 1929 may not have been universal, and that, as in 1957, the general level of gonad ripeness was maintained till winter when a second major spawning took place.

The major spawning in November 1928 is paralleled by a similar spawning in the November sample from the Dove and Bet Reef material. However, since this took place in the laboratory aquaria, and since the December sample showed no signs of a recent spawning, it is evident that it was either only partial, or else brought on by change of environment and handling. It is considered, in view of this and the findings of Nicholls, that the occurrence of this major summer spawning may vary from year to year between the months of November and January (for sea temperatures over observational period, see Fig. 3).

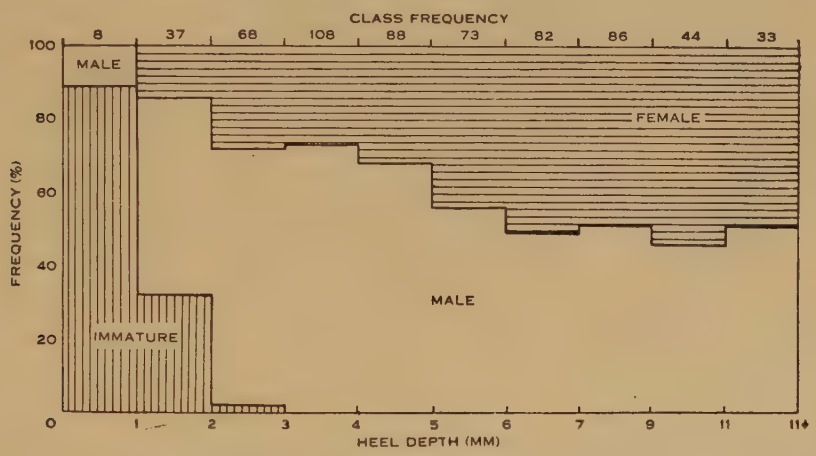

Fig. 4.—*P. margaritifera*: sexual composition of the age groups (based on heel depth) showing the onset of sexual maturity and the increase with age in the percentage frequency of females.

Nevertheless, the basic conclusions already reached remain unchanged:
(1) There are two major spawnings a year, one in summer, one in winter.
(2) Limited spawning may occur at other times.

VII. Age at First Maturity

Represented in histogram form in Figure 4 are the percentages of immature oysters, and mature males and females. The varying proportions of the latter are discussed in Section VIII. Of the youngest oysters, it is seen that, whereas specimens with a heel depth of 1 mm or less are nearly all immature, sexual maturity has been attained in 70 per cent. of specimens of 2 mm heel depth, and in practically all of 3 mm. This assessment of gonad maturity is based on macroscopic observation.

A number of these young oysters were sectioned and histological criteria used for a more reliable determination of maturity. The results are recorded in Table 4.

It is at once evident that many oysters begin to mature at a heel depth of 2 mm or less; nevertheless the average individual is not completely mature till it has reached a heel depth of 2·5–3 mm.

Measurements from several young oysters whose age is approximately known make it possible to interpret such a heel depth in terms of age (Table 5). The maximum age of these specimens (that is, the period of exposure of the collector) is known and, assuming that they originated from a major spawning, it is seen that, on the average, 1-year old specimens are 2 mm in heel depth.

Some individuals, therefore, begin to mature at the end of their first year but, as a whole, the species becomes sexually mature during the first or second breeding season of the second year.

TABLE 4

HISTOLOGICAL DIAGNOSIS OF THE GONAD STATE OF YOUNG OYSTERS, SHOWING THE PRIMARY DEVELOPMENT OF THE GONAD AND THE ONSET OF SEXUAL MATURITY (JULY 1956)

Gonad State	Oyster Size, Expressed as Heel Depth (mm) : Weight (oz) : Dorsoventral Measurement (cm)
i	2·0 : 0·5 : 5·0; 2·0 : 0·25 : 4·7
Mr_2	2·0 : 1·0 : 5·5; 2·0 : 1·0 : 6·3
Md_1	2·0 : 1·0 : 6·3
Md_2	2·0 : 1·0 : 6·0
Md_3	2·0 : 1·5 : 6·7; 2·5 : 1·0 : 6·2
Md_4	2·5 : 1·0 : 5·6; 2·5: 2·0 : 7·2; 2·0 : 1·5 : 6·4; 2·5 : 1·0 : 6·2; 3·0 : 1·0 : 6·4; 2·0 : 1·0 : 6·8; 3·0 : 1·0 : 6·0
Md_5	2·0 : 1·5 : 6·5; 2·0 : 1·5 : 6·8; 3·0 : 1·5 : 6·3
Fd_1	2·5 : 2·0 : 6·8
Fd_5	2·5 : 2·0 : 7·4

VIII. SEXUALITY

Figure 4 shows that, at first maturity, there are approximately five males for every two females and that this ratio progressively decreases until in older groups the proportions are approximately equal. It has been shown (Tranter 1958*c*) that such pronounced variation in sex ratio is the result of sex-change within the population.

In *P. margaritifera*, among the 300 gonads sectioned over a period of a year, two were observed to be clearly bisexual (Table 1). In one of these, the sex was changing from male to female, and in the other (Plate 2, Fig. 10), from female to male. These cases, although rare, are sufficient to confirm that the species is sexually unstable. In both, the developing phase appeared to have arisen very rapidly. In the gonad designated Md_4Fr_2 there was a continuous series of spermatogenic stages from stem cell to spermatozoan; in the gonad Fd_5Mr_1 all oocytes were well formed and healthy. These are conditions met with only when gametogenesis is proceeding at a rapid rate.

It is therefore probable that, had samples been taken more often than once a month, the bisexual condition would have been found in a greater percentage of

cases. On these grounds, and by analogy with *P. albina*, it is considered that the observed variation in sex ratio may be attributed to sex-change; and that the gradual increase in the percentage of females is the result of the more common occurrence of protandric sex-change.

Although Figure 4 does give some idea of the extent of sex-change within the population, one can gauge this accurately only by making continuous observations on individual oysters. Because of limited material it has not been possible to do this with *P. margaritifera*.

TABLE 5

ESTIMATED AGE OF SPAT, SETTING ON COLLECTORS EXPOSED FOR A KNOWN PERIOD (assuming that breeding is in the main biannual)

Collector	Estimated Age of Spat (Months)	Heel Depth (mm)	Dorsoventral Measurement (cm)	Weight (oz)
M. V. *Pelai* (laid 25.v.51, recovered 19.xii.52)	11–16	2·0	9·4	
		1·5	8·4	
		1·0	7·3	
		1·5	9·5	
		1·0	8·2	
		1·0	7·6	
		1·0	8·3	
		1·0	7·5	
		2·0	7·5	
		2·0	8·1	
		2·0	8·5	2
		2·0	7·6	2
		2·0	8·0	2
Cages, Thursday I. raft (laid ?.vi.55, recovered 22.ii.56)	6	1·0	5·0	⅜

Past workers, believing the species to be dioecious, failed to appreciate the significance of the varying sex ratio. Seurat (1904*a*, 1904*b*) reported that males were vastly outnumbered by females: for every 3–4 males there were 50 females. Nicholls (1931), on the other hand, found males to be more numerous (5 : 3). Galtsoff (1933) examined 160 adult oysters from Pearl and Hermes Reef (Hawaii) and noted that 40 per cent were male, and 60 per cent. female. Ranson (1952) found that, in the Tuamotus, the sex ratio varies from place to place.

The only other observations on sectioned gonads of this species were those of Galtsoff (1950). In a sample of 27 adult oysters from Panama, he found one with a bisexual gonad. His figure 27 indicates that sex-change was taking place from female to male.

To summarize, the evidence strongly suggests that *P. margaritifera*, in common with *P. albina* (Tranter 1958*c*), is a protandric hermaphrodite species. Protogynic, as well as protandric, sex-changes occur and it is therefore possible that several sexual phases occur in the life of an individual.

IX. Discussion

In *P. albina* (Tranter 1958*b*) no cases were recorded of germinal vesicle breakdown within the ovary and it was concluded that this takes place during, or immediately after, spawning. In *P. margaritifera*, however, sections of spawning ovaries (Plate 1, Fig. 6) have shown that oocytes become activated while still within the ovarian follicles; but since these were never observed in ripe (unspawned) ovaries (Plate 1, Fig. 4) it is certain that activation takes place *immediately before spawning* and is of very short duration. This would explain why the process was not observed in the *P. albina* material, in which the proportion of females was low.

Brooks (1880) showed that early cleavage in the egg of the American oyster (*Crassostrea virginica*) is characterized by the formation, at the nutritive pole, of an unusual "polar lobe". Since then, such a pattern of cleavage has been shown to occur in many bivalves, and in some gastropods and polychaetes (see Costello *et al.* 1957). Experiments with this structure have played a major part in establishing that there is cytoplasmic prelocalization in the unsegmented egg (Wilson 1925, pp. 1062–7). The fact that it is well developed in pearl oysters (see also Wada 1942, 1953) is therefore of interest.

The present investigations have revealed that *P. margaritifera* becomes sexually mature in the second year. This confirms the opinions of earlier workers: Seurat (1904*a*) supposed that young individuals are capable of emitting spawn, but in smaller quantities; Talavera and Faustino (1931) suspected that spawning occurs in just over a year; Ranson (1952) believed that the oysters begin to spawn at the end of the first year, but doubted whether these gametes are viable; Crossland (1957) reported that breeding commences during the summer of the second year. Although Crossland presented no supporting evidence, his statement must be regarded as authoritative because he had unlimited opportunity to observe the development of gonad in oysters whose age was precisely known. Since *P. albina* becomes sexually mature within the first 6 months (Tranter 1958*a*), and probably spawns twice in the first year, *P. margaritifera* is, by comparison, a late-maturing species.

This may explain why the proportion of females at first maturity is much higher than in *P. albina*; one might possibly find that they have already passed through a phase of incipient maleness.

Spawning intensity in *P. albina* reaches a maximum in autumn, but is high enough in other months to allow a certain amount of breeding; as a result, spat settlement is continuous and heavy spatfalls may occur in any month (Tranter 1958*c*). The reproductive cycle of *P. margaritifera* differs from this, in that there are two major spawnings a year, one in summer, one in winter. Since their spat seldom settle on surface collectors in the Thursday Island area, there are, therefore, no records

of seasonal spatting intensity in this species. Usually, however, there were always a few spawning individuals in the monthly samples (see Table 1) and it is probable that, in this species also, breeding is practically continuous.

This supports the contention (Galtsoff 1933; Tranter 1958*c*) that in the pearl oysters there is a particular threshold temperature which, when exceeded all the year round, permits continuous breeding, and, when exceeded only in summer, restricts breeding intensity to the summer months. For instance, Galtsoff (1933) has shown that, at Pearl and Hermes Reef (27°N.), spawning takes place during the period of maximum sea temperatures (25°–27°C). This is indicated by the fact that, at this time, adult oysters are ripe and can be induced to spawn; length frequency distribution of young oysters confirms this. Crossland (1957) records that, in Dongonab Bay (21°N.), there is no trace of gonad in autumn and winter; it begins to develop about March and by June oysters are ripe; spawning occurs at intervals from July to October, by which month the gonad is once more invisible. Bearing in mind the world distribution of pearl oysters and data relating spawning to sea temperature, it is suggested that this threshold temperature is approximately 23°C.

Other areas in which observations have been made on the gonad of *P. margaritifera* are Panama (7°–9°N.) and Tuamotu (13°–25°S.). Galtsoff (1950) examined 27 adult oysters from Panama during February and March; these were either ripe or spent, which suggested that some degree of spawning takes place during those months. It is possible, of course, that breeding is more intense in other months; the significance of these records is therefore limited.

Many differing opinions have been expressed concerning the breeding season in the Tuamotu Archipelago. Grand (1895) found an abundance of genital products during all seasons. Seurat is reported to have found spawning to be continuous, but most intense between July and October (Ranson 1952). Hervé (1934) agreed with Seurat in the former respect but believed the major spawning season to be October to February. Ranson (1952) agreed with Hervé on the major spawning issue, but declared categorically that the pearl oysters of Tuamotu do not have functional gonads during winter. Although he noticed pearl oyster larvae at this time, he claimed that they were derived from "restes de la dernière saison de reproduction". This is very difficult to believe. Residual eggs are certainly found in the ovary (Plate 1, Fig. 6), but the present author has found that these degenerate and are resorbed shortly after spawning.

The observations of all these workers are unlikely to be faulty, and it seems that there is some variability in the breeding season of the species in that area. In view of the previous discussion, it is highly probable that this variability is the differential response of the species to the range of latitude over which the Tuamotu population is distributed.

The solution of the problem is now important, since the work of Crossland (1957) has shown that *P. margaritifera* can be cultivated successfully in semi-enclosed areas such as Dongonab Bay in the Red Sea. Such an area favours the retention of a large proportion of larvae within the growing area. It is only necessary, then, to provide a suitable settling surface, at the right time and place within the growing area, to ensure a heavy spatfall.

The coral atolls of the Tuamotu Archipelago and Northern Cook Group are eminently suited from these points of view. It is here that the best blacklip shell in the world is found.

X. Acknowledgments

Thanks are due to the Commonwealth Navigation and Lighthouse Service for permission to accompany S.S. *Cape Leeuwin* to Dove and Bet Reefs to collect material, and to the Master of the vessel, Captain Chesterman, for arranging to have the oysters supplied with running sea-water. The work was carried out, in part, at Thursday Island in the laboratory provided by the Queensland Government and maintained by C.S.I.R.O.

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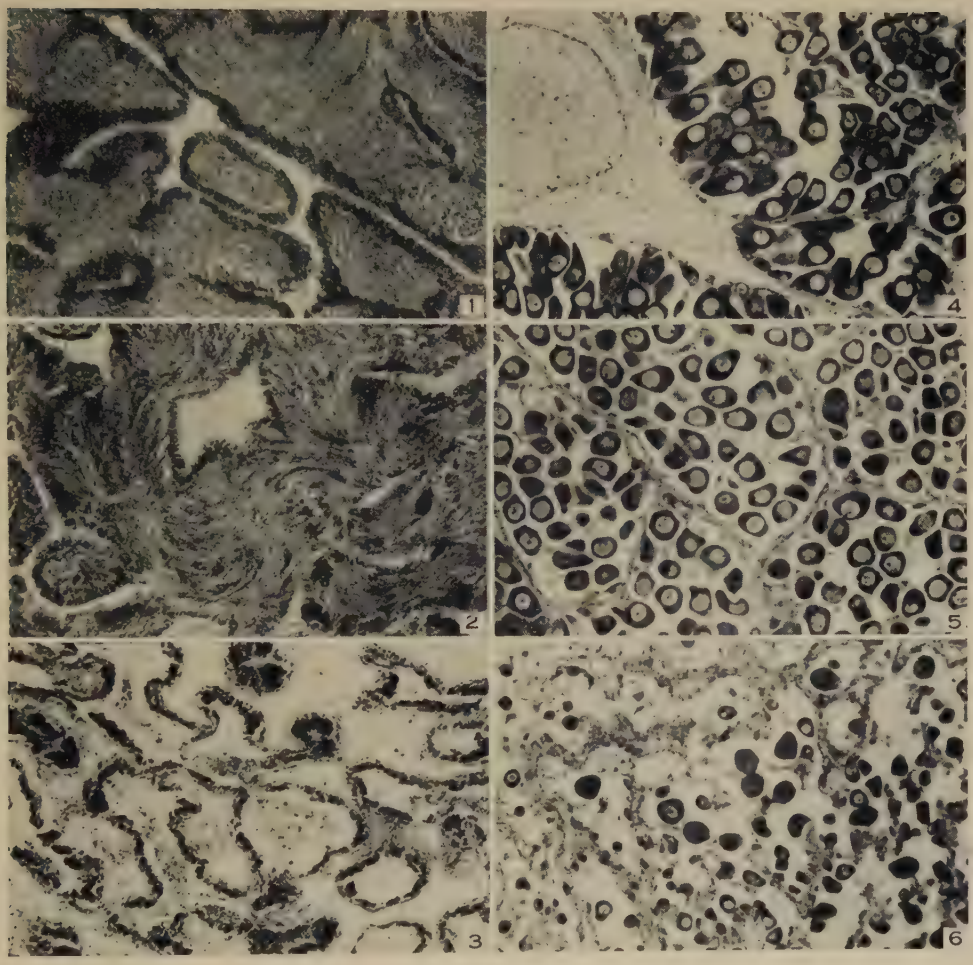
REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. IV



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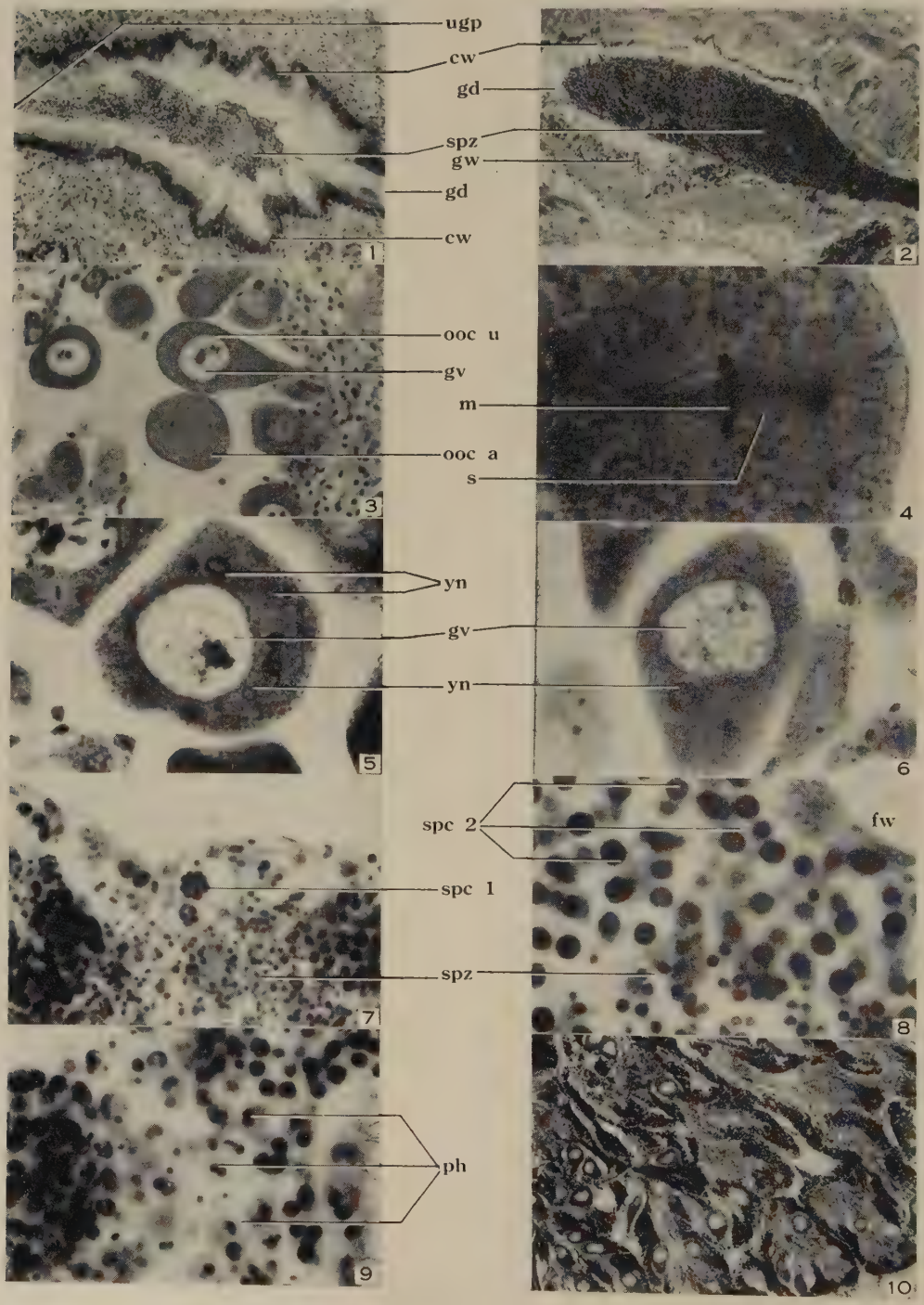
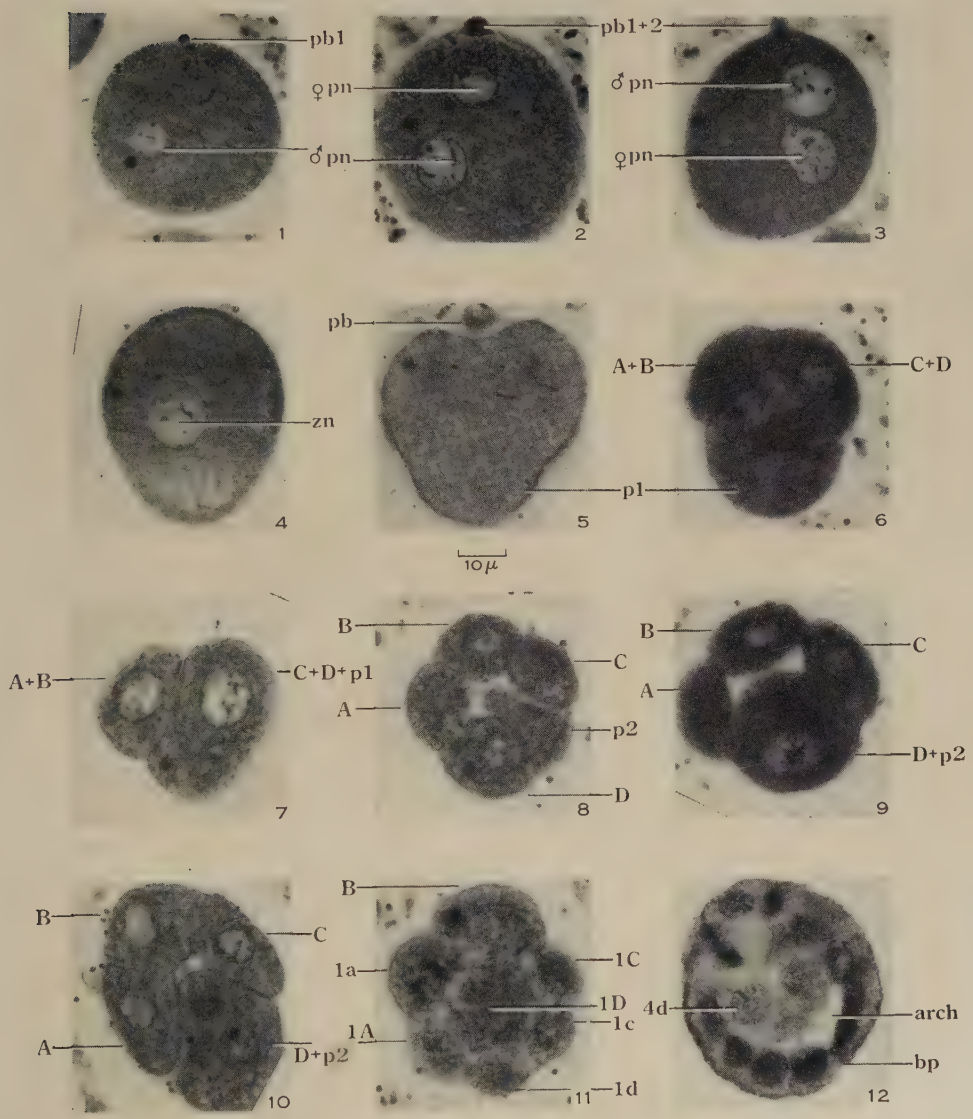
REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. IV



REPRODUCTION IN AUSTRALIAN PEARL OYSTERS. IV

ANIMAL POLE



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EXPLANATION OF PLATES 1–3

arch, archenteron; *bp*, blastopore; *cw*, ciliated wall of gonoduct; *fw*, follicle wall; *gd*, gonoduct; *gv*, germinal vesicle (nucleus); *gw*, germinal wall of gonoduct; *m*, metaphase configuration; *ooc a*, activated oocyte; *ooc u*, unactivated oocyte; *p 1*, *p 2*, polar lobes 1 and 2; *pb 1*, *pb 2*, polar bodies 1 and 2; *ph*, phagocytic cell; *pn*, pronucleus; *s*, spindle; *spc 1*, primary spermatocyte (diplotene); *spc 2*, secondary spermatocyte; *spz*, spermatozoa; *ugp*, urogenital pore; *yn*, yolk nucleus; *zn*, zygote nucleus.

PLATE 1

Histological gonad stages

Fig. 1.—Md_4.
Fig. 2.—Md_5.
Fig. 3.—Mr_3.
Fig. 4.—Fd_4.
Fig. 5.—Fd_5.
Fig. 6.—Fr_3.

PLATE 2

Fig. 1.—Section along urogenital papilla showing the heavily ciliated walls of the urogenital duct. ×70.

Fig. 2.—Section along main gonoduct showing how the walls are partly ciliated, partly germinal. ×70.

Fig. 3.—Section across spawning follicle showing an activated and an unactivated oocyte lying side by side. ×280.

Fig. 4.—Animal pole of activated oocyte highly magnified to show the metaphase configuration. This is the stage at which fertilization takes place. ×1400.

Fig. 5.—Ripe oocyte showing the ring-like cytoplasmic inclusions termed "yolk nuclei". ×700.

Fig. 6.—Oocyte showing single large yolk nucleus. ×700.

Fig. 7.—Section across part of a male follicle showing the unusual late diplotene arrangement of the primary spermatocyte. ×700.

Fig. 8.—Section across part of a male follicle showing the secondary spermatocyte. ×1400.

Fig. 9.—Phagocytic resorption within a spent male follicle. ×700.

Fig. 10.—A bisexual phase (Md_4Fr_2). ×70.

PLATE 3

Fertilization and cleavage

Fig. 1.—The fertilized egg, showing the first polar body and the advancing male pronucleus.

Fig. 2.—After protrusion of the second polar body and the formation of the female pronucleus.

Fig. 3.—Pronuclei immediately before fusion.

Fig. 4.—Immediately after fusion, showing the zygote nucleus. Note that the cytoplasm at the vegetal pole becomes clearer, for a time, and begins to protrude.

Fig. 5.—Early trefoil stage, preceding first cleavage.

Fig. 6.—Late trefoil stage showing the blastomeres $A+B$ and $C+D$ and the cytoplasmic "polar lobe".

Fig. 7.—Later stage showing how the 2-cell stage is formed from the trefoil by fusion of $C+D$ with the first polar lobe.

Fig. 8.—Result of the second cleavage by which are formed the primary blastomeres A, B, C, and D, and a second polar lobe (cut tangentially).

Fig. 9.—Later, showing how the 4-cell stage is formed by the fusion of cell D with the second polar lobe.

Fig. 10.—Another view of the 4-cell stage showing the arrangement of the primary blastomeres.

Fig. 11.—7-cell stage (B has not yet divided).

Fig. 12.—The gastrula.

THE EGG YIELD FROM BROWN AND RAINBOW TROUT IN TASMANIA

By A. G. Nicholls*

[*Manuscript received June* 27, 1958]

Summary

Counts of eggs stripped from brown and rainbow trout show that over a sufficiently large size range the relationship to fish length is curvilinear. A direct relationship exists between egg numbers and fish weights. Brown trout from the Great Lake do not yield the expected number at larger sizes. The yield from rainbow trout is higher than that from brown.

I. Introduction

The relationship between the size of fish and the number of eggs they yield is a matter of some interest in stripping fish for hatchery purposes, as well as in studying fish populations and their potential for reproduction. This subject has already been considered to some extent by workers in New Zealand, Canada, and the United States of America, but because of the different conditions in Tasmania it seemed advisable to consider it here in relation both to results from other countries and to variations within this State.

The stripping of fish for hatchery purposes has been conducted at three main centres in Tasmania during the past decade, at places where fish traps are installed. One is in the Plenty River, a tributary of the Derwent River about 30 miles from Hobart, and the others are on the main sources of water flowing into the Great Lake and Lake Leake, up which fish migrate for spawning. These will be described in greater detail in later papers dealing with the fishery of these regions.

II. Methods

The Plenty River carries mainly brown trout; a few rainbow occur but they are insufficient in number to provide a spawning run. The two lakes carry populations of both species. At each spawning run, over a period of several years, batches of 10 fish were stripped and the eggs counted separately, at intervals during the run. It was essential that only fish which were carrying their full complement of eggs should be used for this purpose, but in some cases part-spent fish were recorded; these have been omitted from consideration here. However, there is a considerable range in the number of eggs per fish and it is possible that some of those included had in fact shed some of their eggs before stripping. The process of stripping is not always as complete as natural spawning, and it is probable that some eggs may have remained within the fish; this may occur also in natural spawning (Stuart 1957).

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The results given here may be regarded as representing reasonably accurately the numbers which may be stripped from fish of a given size, rather than the true number carried by the fish; the results should be of value for comparative purposes. A count of the ova in the ovary, the method employed by Ricker (1932), by Smith (1947), and by Allen (1951), would represent the latter more accurately but involves the death of the fish.

Fish were measured to the nearest centimetre (fork-length) and were weighed before and after stripping to the nearest quarter ounce; weights have been converted to grams and rounded to the nearest 10 g, and egg counts have been rounded to the nearest 10. Any errors introduced by the methods may probably be ignored in view of the considerable range in number of eggs found in females at any given size. Ricker (1932) found that in *Salvelinus fontinalis* the upper limit was about twice the lower; in the present case the upper limit may be up to three times the lower in both brown and rainbow trout.

In the statistical treatment, statements that differences were significant, quite significant, or highly significant, refer to significance at the 0·1 per cent. level; for lower levels of significance the values are given in the text.

III. Results for Brown Trout

(a) *Plenty River*

Fish trapped in the Plenty River have been studied since 1952, but egg numbers are available for only the first four seasons, from a total of 85 fish.

(i) *Length Relationship.*—This was found to be clearly curvilinear. Tests on a linear regression fitted to the data showed a significant deviation from linearity, and curvilinear regressions were fitted according to the equation $N = aL^b$, in which N represents the number of eggs per fish of length L, and a and b are constants. In those seasons where the number of observations exceeded 20, the correlation of the points about the logarithmic regression was excellent; in the one season in which the value of the correlation coefficient (r) was not significant, there were only 12 sets of data. Statistical comparison between the logarithmic regressions for each season showed no significant differences in either slope or distance apart and the results have therefore been pooled to express the relationship at this source. When the logarithms of egg numbers are plotted against fish lengths the points lie about a straight line with a high degree of correlation. The mean values for the pooled data are plotted in Figure 1, to which the curved line has been fitted.

(ii) *Weight Relationship.*—The distribution of points in this relationship clearly falls about a straight line and for each season with over 20 observations the value of r is quite significant. A comparison of the regressions between seasons showed no significant difference in either slope or distance apart and the results may therefore be pooled with confidence to express the relationship at this source. The correlation of the pooled data was very good, and the mean values are plotted in Figure 2. Values for two fish, one at 2·5 kg with 4140 eggs and the other at 6·5 kg with 7850 eggs, have been omitted from this Figure; the former departs from the calculated value by nearly 30 per cent. but the latter by only 4 per cent.

(b) *Lake Leake*

From the spawning runs at Lake Leake from 1952 to 1955 data are available from 119 fish.

(i) *Length Relationship.*—Regressions calculated for each season do not differ significantly from one another in slope, and only at the 5 per cent. level in their distance apart. Since there is no indication of any seasonal trend it is concluded that the results for four seasons may be pooled. Correlation within seasons is good for two of the seasons and for the pooled data it is quite significant. The latter show no significant deviation from linearity and clearly fit about a straight line. Mean values are plotted in Figure 1.

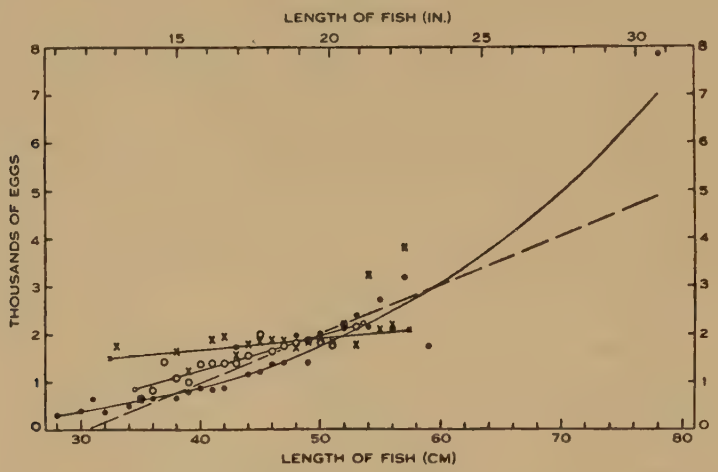

Fig. 1.—Mean number of eggs and length of brown trout; pooled results for four or more seasons. ●, Plenty River; ○, Lake Leake; ×, Great Lake.

(ii) *Weight Relationship.*—When egg numbers are plotted against fish weights a straight-line relationship is clearly indicated (Fig. 2). Correlation within seasons is reasonably good and comparison of the regressions between seasons shows no significant difference in either slope or distance apart, so that the results may be pooled to represent the relationship at this source. The correlation of the pooled data is quite significant.

(c) *Great Lake*

During the six seasons from 1952 to 1957 data are available from 273 fish.

(i) *Length Relationship.*—Correlation of the points within seasons is very poor except for one season. Statistical analysis of the differences between the regressions between seasons indicates a difference in slope significant at the 1 per cent. level. This is due to one season in which only 18 fish were sampled; it may be regarded as a sampling error. When this season is omitted there is no significant difference in slope but there are differences in the distance apart which are significant at the

0·1 per cent. level. It has been decided to use the pooled results for all six seasons since there is no evidence of any seasonal trend and no significant difference between the regressions for the five pooled seasons and the six pooled seasons, in respect of either slope or distance apart. Since the sets of data for the aberrant year number only 18 in a total of 273 it does not appear likely that their inclusion would seriously affect the conclusions, and correlation, though not very good in either case, is better for six seasons than for five. The pooled data show no significant deviation from linearity and mean values have been plotted in Figure 1 together with the regression for the six seasons.

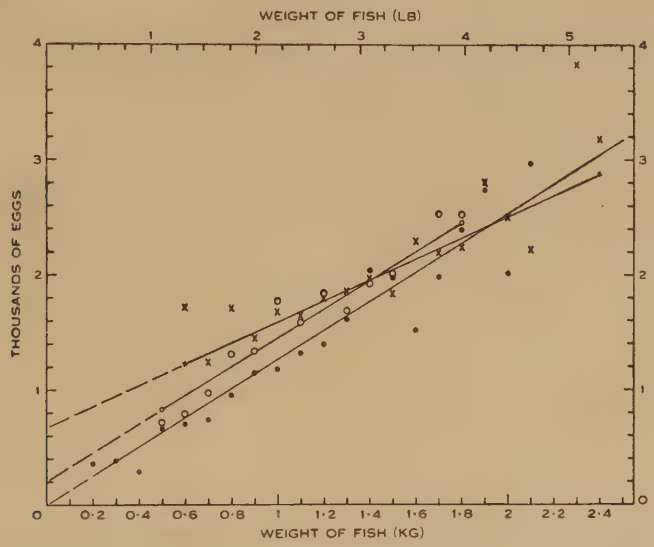

Fig. 2.—Mean number of eggs and weight of brown trout; pooled results for four or more seasons. ●, Plenty River; ○, Lake Leake; ×, Great Lake.

(ii) *Weight Relationship.*—Correlation within seasons is good for only three. Comparison of regressions between seasons shows a difference in slope significant at the 1 per cent. level, and the exclusion of the 1955 sample of 18 fish, which has a steeper slope than the other seasons, results in no significant difference being found between the samples for the remaining years. The distance separating these is significant at the 1 per cent. level. There is no significant difference in either slope or distance apart between the pooled data for six seasons and for five seasons, and the correlation of the points is quite significant in both cases and a little better for six seasons than for five. No seasonal trend is to be seen and it is probable that the pooled data for all seasons will represent the relationship with reasonable accuracy (Fig. 2).

(*d*) *Comparison between Sources*

It has been shown that in each case the pooled data may be accepted as representing the relationship with reasonable accuracy.

(i) *Length.*—While the data for the Plenty River fall about a curve those for the two lakes fall about straight lines. In order to make a comparison it is necessary to express the results from all sources by the same method, and in Figure 1 the broken line represents the linear regression for the Plenty River data. It is clear that this line has a steeper slope than that for Lake Leake, which in turn is steeper than that for the Great Lake, indicating a greater difference with increasing length of fish. The difference between each pair of coefficients is significant.

(ii) *Weight.*—Figure 2 shows that the regression for Lake Leake is parallel to that for the Plenty River, but stands at a higher level; in neither the slope nor the distance apart is the difference significant. The regression for the Great Lake shows a slope which is significantly different from that for the Plenty River, but it does not differ from that for Lake Leake, neither is the distance separating the two significantly different. The pooled data from these two sources will give a mean value for brown trout from these two lakes over the period in which they were studied.

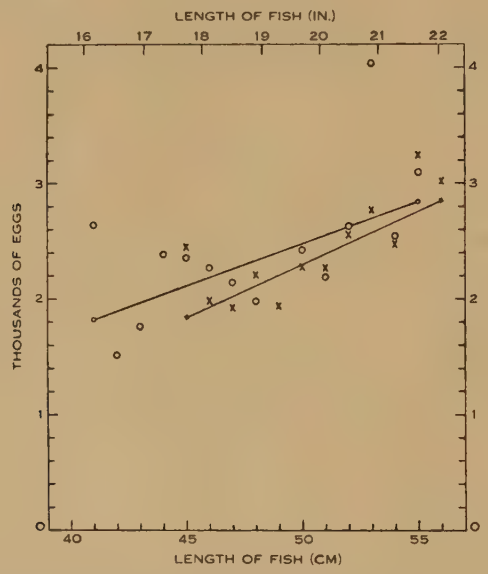

Fig. 3.—Mean number of eggs and length of rainbow trout; pooled results for four seasons. ○, Lake Leake; ×, Great Lake.

IV. Results for Rainbow Trout

(*a*) *Lake Leake*

Data are available from 64 fish taken during the four seasons from 1952 to 1955.

(i) *Length Relationship.*—Within seasons there is in each case a poor correlation owing to the scatter of points, but the regressions show no significant difference in slope. They are significantly different (at the 0·1 per cent. level) in their distance apart, but no trend is indicated. The regression based on pooled samples is used to represent the relationship at this source (Fig. 3), for which the correlation is better, being significant at 5 per cent.; there is no significant deviation from linearity.

(ii) *Weight Relationship.*—For only one of the four seasons is the correlation significant, in the other cases the scatter of points is too great. The regressions are not significantly different in slope but the distances separating them are significantly different at the 0·1 per cent. level. This is probably of little importance in view of the scatter in three of the seasons, and the results have been pooled to represent the relationship (Fig. 4). The correlation of the pooled data is quite significant, suggesting that pooling is justified.

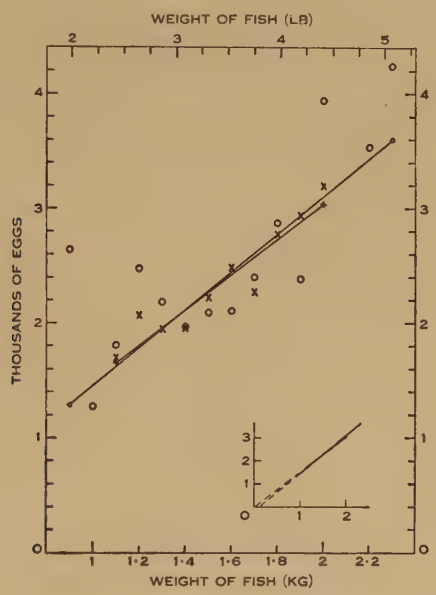

Fig. 4.—Mean number of eggs and weight of rainbow trout; pooled results for four seasons. The inset shows how closely the extrapolated lines approach the origin. ○, Lake Leake; ×, Great Lake.

(*b*) *Great Lake*

From this source data are available from a total of 71 fish taken during four seasons.

(i) *Length Relationship.*—Within seasons the scatter of points is considerable and the correlation poor; it is not significant in any case. Comparison of the regressions between seasons shows no significant difference in either slope or distance apart, so that the data for all seasons can be safely pooled (Fig. 3). Correlation of the pooled data is significant at the 1 per cent. level and there is no significant deviation from linearity.

(ii) *Weight Relationship.*—Correlation of the points within seasons is good for two seasons only, and because comparison of the regressions between seasons shows no significant difference in either slope or distance apart, the data have been pooled (Fig. 4). Correlation of the pooled data is quite significant.

(c) *Comparison between Sources*

Similar numbers of fish were available from each source, and the pooled results will be used for comparison.

(i) *Length.*—There was some scatter of points in both cases, but their correlation was better for the Great Lake (significant at the 1 per cent. level) than for Lake Leake (significant at the 5 per cent. level). When the regressions of the pooled data are compared (Fig. 3) no significant difference is found in either slope or distance apart. The pooled data will serve to indicate the mean number of eggs in relation to length for comparison with the brown trout.

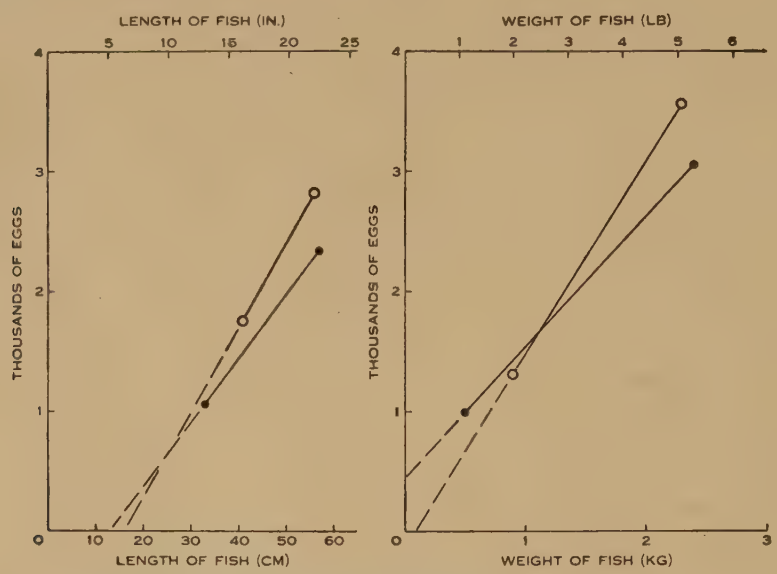

Fig. 5.—Regression lines for pooled data from lakes; ●, brown trout; ○, rainbow trout.

(ii) *Weight.*—In this case there is a high degree of correlation for pooled data from both sources, correlation being significant in each case. Regression lines are very similar in slope (Fig. 4) and there is no significant difference in either slope or distance apart between the two sets of pooled data. Pooled data for rainbows will be used for comparison with brown trout from these lakes.

V. Comparison between Brown and Rainbow Trout

The pooled data for all brown and all rainbow trout from lake sources can be compared mathematically, since the differences within species, if any, are only concerned with the distance separating statistically parallel regressions.

(i) *Length.*—Mean values and regression lines for brown and rainbow trout from the lakes are shown in Figure 5. Correlation of the points about the lines is significant. Although the lines diverge the difference in slope is not significant, but the distance between the lines is quite significant.

(ii) *Weight*.—Mean values and regression lines for brown and rainbow trout are plotted in Figure 5; there is a highly significant correlation of the points about their respective lines. The difference in slope between the two lines and the distance between them are significant at the 1 per cent. level.

VI. Discussion

It is surprising how little factual data on the number of eggs produced by brown or rainbow trout have been published. Their importance in fisheries biology and the inadequacy of the available information have been mentioned by Lagler (1950). Carlander (1950, 1953) cites 22 works of which 10 refer to brown and 17 to rainbow trout. Relatively few of these are based on direct counts of eggs in gravid females or of eggs stripped at hatcheries. Lagler also quotes figures from various American sources, but these are related to the age of the fish and not to their size. Since fish of the same age from different sources can be very different in size, it would seem of greater value to refer egg counts to size rather than to age. Stuart (1957) gives figures for direct counts of eggs yielded by spawning brown trout.

Smith (1947), studying egg production in *Salvelinus fontinalis*, stated that the number of eggs was "related to the weight or volume of the fish rather than to the length". Vladykov (1956) gave data on egg counts in *S. fontinalis* in Quebec, and in the length relationship the points fall about a curve which in shape "is very similar to that of Ontario fish mentioned by Ricker (1932)". His table 16 sets out the relationship from which it can be seen that the numbers increase approximately as the cube of the fish length. Simpson (1951) studying fecundity in the plaice shows that it is related sufficiently nearly to the cube of the length and is thus directly proportional to fish weight. Hickling (1940) found a value for herring in which egg numbers increased at a rate somewhat higher than the cube (3·465). Foerster and Pritchard (1941) expressed the relationship in sockeye and pink salmon by straight lines, but pointed out that they were dealing with fish of a limited size range, restricted to the top part of what was probably a logarithmic curve. In general, where a sufficient size range has been studied within a species, egg numbers increase as the cube of the length or better.

Allen (1951, p. 90) counted the number of developing eggs in brown trout and found that the relation between egg number and fish weight was definitely curvilinear, but that egg number plotted against fork-length gave a reasonably good fit to a straight line. The curvilinear relationship for brown trout from the Plenty River (Fig. 1) is similar to that given by Ricker (1932, fig. 4) for *S. fontinalis*, but at a lower level of production. (This species has a higher egg yield than brown trout.) The apparent conflict between Allen's results for the Horokiwi River and those for the Plenty River, both relating to brown trout, is probably due to the relatively short range of fish lengths over which Allen obtained data (22–38 cm) compared with that for the Plenty River (28–58 cm, with one at 78 cm). Over a short range the data fit well enough to a linear regression because of the great variability in numbers at any one length. This was evident here and is shown to some extent in the counts made by Stuart (1957) although his values are more consistent, with only small variation. They appear to fit reasonably well to the curves for length and weight

for the Plenty River fish, for which the calculated value of the equation is $N = 0 \cdot 00883\ L^{3 \cdot 118}$. This is close to the generally accepted cube relationship between length and weight, an approximation, and it is to be expected that egg numbers will be directly proportional to fish weight.

Tests for deviation from a linear regression on the Plenty River data, for a range similar to that of the Horokiwi River fish, show no significant deviation and and it would be reasonable to fit a linear regression, but in each set of data reported here the correlation of egg number with weight of fish was appreciably higher than the corresponding correlation with length. The curvilinear relationship shown for brown trout in the Plenty River is statistically well founded, and supports evidence from elsewhere. It is suggested that this is normal and that the linear relationship shown for the two lakes was due to other causes, possibly to the shorter range in length over which counts were made. If this is the whole cause then comparison of the linear regressions for the fish from each lake with those from the Plenty River over the same size range as found in each lake should show no significant difference. For the Lake Leake fish there is a difference in slope significant at only the 5 per cent. level, and no significant difference in the distance between the lines, and it may be accepted that the absence of curvilinearity is related to the short range of fish lengths. Fish from the Great Lake show a quite significant difference in slope, and since the range of fish lengths was greater than that for Lake Leake the absence of curvilinearity in this case is not related to the range of fish lengths. It may be concluded that while egg production in Lake Leake fish is similar to that of the Plenty River fish, that of the Great Lake fish is quite different; it will be noted that the difference is due to the larger fish failing to produce the greater number of eggs which could be expected.

The linear regressions for the weight relationship for brown trout (Fig. 2) represent the true relationships in all cases, and it will have been noted that while there is no significant difference between the Lake Leake and Plenty River fish, those from the Great Lake differ significantly from the river fish. The fact that the extrapolated lines for the Plenty River and Lake Leake pass very close to the origin indicates that the relationship is direct. The higher value of the negative intercept on the weight axis for Great Lake fish, together with the less steep slope, indicates a falling off in the egg yield of heavier fish. If the high values found for the lighter fish are a true indication of greater productivity in fish from this lake, this should have been maintained and the line should have risen more steeply than that for Lake Leake fish. It is clear that Great Lake fish do not produce their expected quota of eggs as they become larger, and this will be discussed in a later paper.

The linear regressions for the length relationship in rainbow trout (Fig. 3) may be accepted as a satisfactory fit over the range of fish lengths available from both sources. In neither this relationship nor that for weight (Fig. 4) is there any significant difference between the sets of data and it may be concluded that there is no difference in egg production for rainbow trout at these sources. In both cases the extrapolated regression lines intercept the weight axis close to the origin, indicating a direct relationship. Figure 5 shows that rainbow trout produce a greater number of eggs in relation to their length and weight than do brown trout in the two lakes compared here. From figures quoted by Carlander (1950) the mean number of eggs is about

TABLE 1

SUMMARIZED DATA ON NUMBER OF EGGS, LENGTH, AND WEIGHT OF FISH

Source	No. of Fish	Length of Fish		Weight of Fish		Number of Eggs		Regression Equations for	
		Mean (cm)	Range (cm)	Mean (g)	Range (g)	Mean	Range	Length $N =$	Weight $N =$
Brown Trout									
Plenty River	85	44·9	28–78	1167	200–6460	1479	220–7850	†	$1\cdot27(W - 1\cdot56)$
Lake Leake	119*	44·5	35–53	1092	480–1830	1570	510–3000	$70\cdot99(L - 22\cdot39)$	$1\cdot25(W + 163\cdot84)$
Great Lake	273	47·1	33–57	1275	620–2440	1854	450–3730	$24\cdot32(L + 29\cdot14)$	$0\cdot91(W + 756\cdot39)$
Lakes combined	392*	46·3	33–57	1219	480–2440	1768	450–3730	$53\cdot30(L - 13\cdot14)$	$1\cdot09(W + 409\cdot81)$
Rainbow Trout									
Lake Leake	64	48·8	41–55	1565	940–2270	2388	720–4310	$73\cdot36(L - 16\cdot22)$	$1\cdot65(W - 133\cdot30)$
Great Lake	71	50·7	45–56	1565	1080–2040	2371	1160–3950	$91\cdot58(L - 24\cdot84)$	$1\cdot54(W - 22\cdot20)$
Lakes combined	135	49·8	41–56	1565	940–2270	2379	720–4310	$71\cdot21(L - 16\cdot39)$	$1\cdot60(W - 81\cdot83)$

*Number of fish weighed; the number measured was one less.

†Curvilinear relationship: $\log N = 3\cdot118(\log L - 0\cdot659)$.

1200/lb for rainbow and about 900/lb for brown trout. The corresponding values for fish from sources reported here are somewhat lower.

The results of this study are summarized in Table 1, from which expected egg numbers in relation to length or weight of fish can be calculated.

VII. Acknowledgments

The assistance given by the hatchery staff of the Salmon and Freshwater Fisheries Commissioners who made the fish measurements and egg counts, and by Mr. P. Sprent of the University of Tasmania who gave help with the statistical treatment, is gratefully acknowledged.

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THE STATUS OF THE "WHITE" CRAYFISH IN WESTERN AUSTRALIA

By R. W. George*

[*Manuscript received June* 30, 1958]

Summary

The pale-coloured "white" marine crayfish which occur seasonally along the southern part of the Western Australian west coastal shelf are recently moulted immature crayfish, and are stages in the development of the Western Australian commercial crayfish *Panulirus longipes*. It is suggested that individuals which reappear as whites the following season have failed to mature in the intervening period. During these phases, the average annual increment is about 0·3 in. in carapace length. Crayfish in this phase had carapace lengths from $2\frac{3}{8}$ to $3\frac{3}{4}$ in.

I. Introduction

In onshore coastal waters of Western Australia from Carnac Island to the Geraldton area (Fig. 1), there is a seasonal crayfishery which is based substantially on the capture of pale-coloured crayfish, commonly termed "whites". These regularly appear in considerable quantities during late November and in December and have been regarded by various local authorities as either a species distinct from the commercial crayfish, *Panulirus longipes*, caught at this and other times of the year, or the same species passing through a lighter-coloured phase at that time of the year.

This paper deals with the biology of the "white" crayfish and its relationship to the commercial "red" crayfish identified as *Panulirus longipes* (Milne Edwards).

II. Materials and Methods

In recent years, tagging programmes during the white crayfish season have been conducted from professional fishing boats to assess the movement, colour change, and growth rates of these crayfish. Each crayfish was marked by punching a distinctively shaped hole through the telson, and as each fisherman was issued with separate pairs of marking pliers, each with a different type of mark, the area and the time of release of animals subsequently recaptured could be established.

During November and December 1953, fishermen in five areas tagged approximately 20,000 white crayfish which measured less than the legal length of $2\frac{3}{4}$ in. carapace length. In December 1954 and 1955 tagging was carried out in the Carnac Island area from only one boat, and in December 1956 these fishermen in the same area and a fisherman in the Geraldton area continued the tagging of the white crayfish.

Before the commencement of the white crayfishing season, catches by commercial craypots are poor, and consequently direct underwater collections and observations at that time were necessary. A self-contained underwater breathing apparatus was used satisfactorily on these occasions.

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The length measurement used in this paper is that of the carapace only, measured from the rear of the supra-orbital horns to the mid-dorsal posterior margin of the carapace.

III. Results

(a) *Colour*

Two terms, red and white, have been used by fishermen, exporters, and processors to designate crayfish of different background colour. The term "red" refers to crayfish which range from a deep pink through red-brown to a very deep maroon

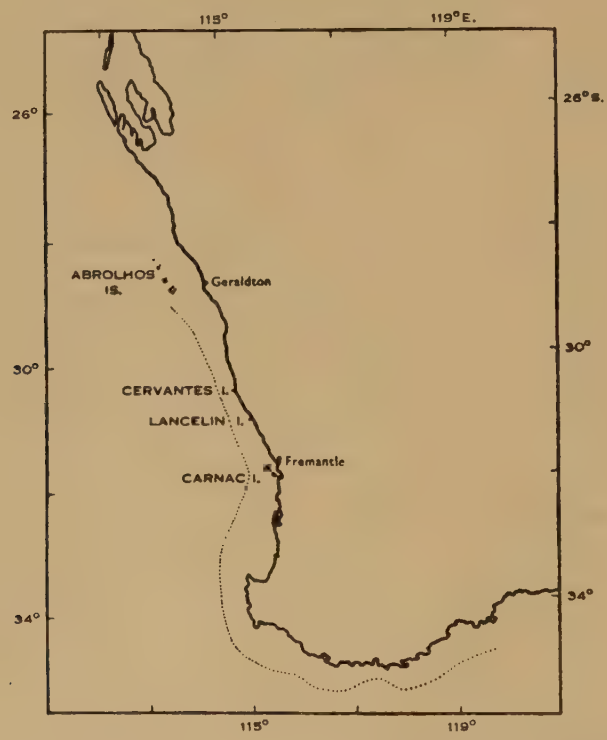

Fig. 1.—Coastline of south-west Western Australia showing areas fished for crayfish.

(almost black) colouration. Those much paler pink crayfish caught at only one period of the year (late November and in December) are referred to hereafter as "whites". Towards the end of the period in which whites are caught the colour of the white crayfish tends to deepen and these crayfish are often referred to as "pinks".

Crayfish considerably paler than reds are also occasionally caught in relatively low numbers at other times of the year. These, however, are not regarded as white by the fishermen or the present author. They are generally associated with a particular substrate, are larger than whites and are usually mature (cf. immaturity of whites—Section III(*c*)).

Irrespective of whether the background colouration is white, pink, or red, crayfish possess a similar pattern of creamy white spots and stripes disposed as follows: single large spots along the lateral margins of abdominal terga 2–6 with smaller spots arranged transversely across the abdominal terga; creamy white tips to the lateral tergal spines, and to the larger spines of the carapace and antennae; and usually stripes but sometimes blotches along the dorsal and lateral surfaces of the peripods.

(*b*) *Length Frequency and Sex Ratio*

Length measurements made during the white crayfishing season indicate that very few whites caught in craypots measure less than $2\frac{1}{2}$ in. or more than $3\frac{1}{2}$ in. (Fig. 2). This is not due to selective sampling by commercial craypots as reds of smaller and

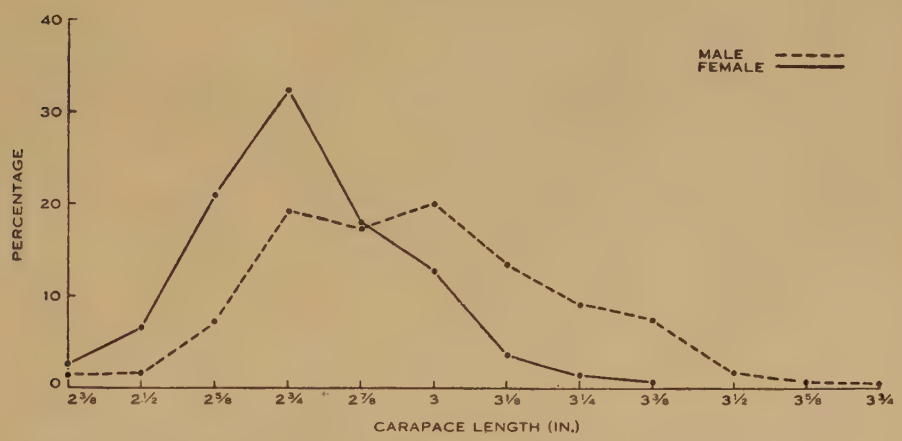

Fig. 2.—Carapace length frequency, whites, Lancelin Island, December 9–13, 1952.

larger sizes than these were also taken during that period. The examination of samples obtained from professional crayfishing boats at several areas indicates that the percentage of whites below the legal length of $2\frac{3}{4}$ in. carapace length varies with the locality and from year to year. The sample from a Lancelin Island boat in 1952 contained 21 per cent. undersized whites (Fig. 2), whereas the corresponding figures for samples obtained from a Carnac Island boat were 9·3 in 1954 and 0·2 per cent. in 1955.

The sex ratio of the Lancelin Island sample approached unity (494 males and 481 females). Further sampling at Geraldton and in the Fremantle area in 1954 and 1955 showed 48 and 52 per cent. males respectively. These figures suggest equality in the sex ratio of white populations. A similar sex ratio was also found at the Abrolhos Islands during the continuous crayfishing test periods of 1948 and 1953 (Sheard 1954; George 1957).

The number of reds processed at factories during the white season is low (about $1\frac{1}{2}$ per cent. at Geraldton in 1956) and males predominate because legal-sized females are usually egg-bearing at this time and by law must be returned to the sea.

(c) *Reproductive State*

For the purposes of this paper, females are regarded as mature if they possess (1) ripening ovaries and an unbroken spermatophore on the last thoracic sternite; or (2) eggs visible externally, adhering to filaments on the margins of pleopods, i.e. on the "breeding plumage" described by Sutcliffe (1953); or (3) spent and inactive ovaries, with or without egg remnants on the filamentous pleopods.

The majority of mature reds (females) during late November and December can be placed in the second category, i.e. eggs visible externally. Female whites, regardless of size, possess none of the above criteria indicative of maturity, but, in contrast, have thin white strap-like ovaries and non-filamentous pleopods indicative of immaturity. No data on the reproductive state of male white crayfish were collected.

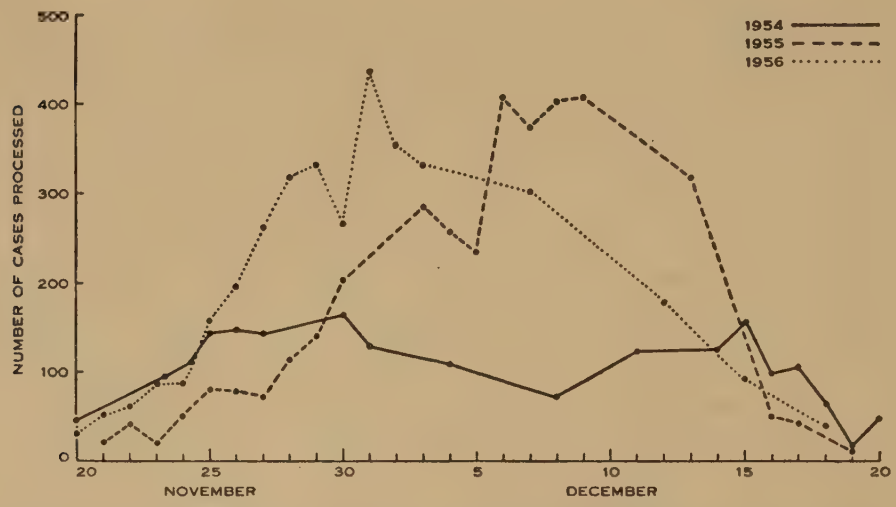

Fig. 3.—White crayfish production figures, Geraldton factory 1954, 1955, 1956. Only production figures of daily catches from craypots which have fished for 24 hours are included (see text).

Recent investigations of the size at which red females mature showed that few females were mature below 2·65 in. carapace length and that at 3·05 in. all females were mature; the size at which 50 per cent. maturity is attained is roughly estimated at 2·70 in.

(d) *Moulting and Colouration*

Factory examinations of whites at the beginning of the white season have shown that all are recently moulted and possess a clean shell, free of fouling organisms commonly found on the shell of premoult or intermoult crayfish.

The regularity of the moult period, and thus of the commencement of the white season, is illustrated in Figure 3 which records the daily number of cases of whites processed for 1954, 1955, and 1956 at the largest Geraldton factory. Where fishing

was disrupted by adverse weather, production figures for those days and for the day following the disturbance have been omitted, i.e. the figures represent catches from craypots which have fished for 24 hours only. In 1956, recently moulted whites were first caught on November 23 and maximum numbers were reached on December 1.

On November 11, 1956, when catches by pots were negligible, the underwater breathing apparatus was used to collect, by spearing, 65 crayfish in two areas (*A* and *B*) in Chapman Bay, Geraldton. These were sexed, measured, and the moult condition recorded (Table 1).

TABLE 1

CARAPACE LENGTH OF CRAYFISH COLLECTED CHAPMAN BAY, GERALDTON

On November 11, 1956. Total collected, 65

Carapace Length (in.)	Area *A*, Reds (6 ft)				Area *B*, Whites (15 ft)			
	Premoult		Recent Moult		Premoult		Recent Moult	
	♂	♀	♂	♀	♂	♀	♂	♀
1·95		1						
2·05								
2·15	2	1	1	2				
2·25				2				
2·35	1		1	4				
2·45		2		1				
2·55	1	2	1	2				
2·65			1					
2·75	2			1				3
2·85						2		
2·95					1	1	2	2
3·05					3	2	3	1
3·15					2	2	1	3
3·25					2	1	1	
3·35					1		1	
3·45					1			
3·55							2	
Totals	6	6	4	12	10	8	10	9

(i) In area *A* (6 ft in depth) only red crayfish were found. Approximately 50 per cent. of this sample were newly moulted and the remainder were approaching a moult and possessed a new red shell beneath the old red shell. The carapace length range was 1·9–2·7 in.

(ii) In area *B* (depth 15 ft), the crayfish measured between 2·7 and 3·5 in. carapace length; 50 per cent. were white, possessing freshly moulted pale-coloured shells, while the remainder consisted of crayfish, obviously near ecdysis, having soft white shells covered by old red shells.

It thus seems that mid November is a general moulting period, at least for crayfish of the sizes sampled (1·9–3·5 in.) and also that whites are not a species distinct from the reds, but are, in fact, animals in one of the many moult phases in the life history of the crayfish *Panulirus longipes*. As additional evidence, some crayfish marked in the white phase have been recaptured as reds, while penned whites have deepened in colour to reds after 2 months. Further circumstantial evidence that whites become reds is the change in colour of the crayfish towards the end of the white season. At this time they are pink and later, when in the words of the fishermen "the whites are gone", only reds are caught.

If the crayfish sampled in the two areas at Geraldton are representative of the condition of the general white population in adjoining areas, the time lapse between moulting (November 11) and the resumption of feeding as indicated by the first entry into craypots (November 23) is at least 12 days, since it is logical to assume that the first crayfish to moult are the first to enter craypots. This period, although obviously a less reliable estimate than that obtained by direct observation on individuals, does approximate to the time lapse recorded by several workers on other species of *Panulirus*. For *P. interruptus* (Randall), Lindberg (1955) observed feeding to recommence 7–9 days following the moult and according to Smith (1951) this period for *P. argus* (Latreille) is 12 days. Travis (1954), however, working with *P. argus*, observed a period of 5–6 days for initial hardening of the newly moulted shell, after which feeding began.

(*e*) *Accumulation and Dispersal of White Crayfish*

Underwater examination of some Geraldton coastal areas, before and after the whites first appear in craypots further offshore, shows that there is an accumulation of premoult (pre-white) crayfish close to the shore early in November. Following the general mid November moult, relatively few whites were observed in these shallow coastal situations. These observations suggest an onshore movement of pre-white crayfish and an offshore movement following the moult. The following results of marking support this latter suggestion.

During December 1953, approximately 2000 undersized whites were marked and released within 4 miles of the coast near Cervantes Island. Following normal fishing practice, the craypots were gradually moved further offshore and during these shifts, marked crayfish were recaptured in diminishing numbers each day. The most westerly recapture was 8 miles offshore (4 miles west of the release area) within 14 days of release. Short-term recaptures of marked, undersized whites in the Carnac Island area in 1954, 1955, and 1956 indicated a similar dispersal pattern to that which occurred in the Cervantes area.

During the 1955 and 1956 white seasons, 66 of the 1770 crayfish marked in the Carnac Island area during December 1954 were recaptured in the same general area, and of the 63 long-term recaptures in 1955, 61 were white and the other two were red. In 1956, only three crayfish, marked as whites in 1954, were recaptured and these were still white.

To sum up, it seems that after moulting in mid November, the exoskeleton gradually hardens and the whites vacate the shore areas, moving offshore into

deeper waters. Here they enter the craypots of the fishermen as recently moulted whites towards the end of November. These whites gradually deepen in colour, possibly entering the red population; some may return to the shallows in following seasons as pre-whites, becoming white again with the November moult.

(*f*) *Growth*

The marking of white crayfish outlined in Section II was designed to give information on the mass movement of crayfish; the marked crayfish recaptured could not be recognized individually. Growth from season to season can be inferred only from a comparison of mean lengths of samples when marked and when recaptured in successive seasons.

TABLE 2

GROWTH OF RECAPTURED WHITES, TAGGED AT CARNAC I. DURING DECEMBER 1954

Carapace Length (in.)	Undersized Sample, December 1955		Whites Recaptured, December 1955		Whites Recaptured, December 1956	
	♀	♂	♀	♂	♀	♂
2·55	2					
2·65	8					
2·73*	19	3				
2·75			1			
2·85			6			
2·95			20	2		
3·05			13	3		
3·15			7	2		
3·25			2	2	1	
3·35				2	1	1
3·45				1		
Mean	2·69	2·73	3·00	3·17	3·30	3·35
Combined Mean	2·70		3·03		3·32	

*Adjusted centre representing crayfish between 2·70 and 2·75 in. carapace length.

The 1770 white crayfish released in December 1954 were not measured, but they were undersized and therefore all less than the legal length of 2·75 in. In order to establish a base line from which average growth could be calculated, a sample of 32 undersized whites was measured in December 1955.

This sample had a mean of 2·70 in. and it is this figure which is used as the base line for growth estimates on the assumption that it is representative of the undersized crayfish released the previous year. In this case, considering a white crayfish length frequency curve such as that obtained at Lancelin Island in 1952

(Fig. 2) the mean length of the crayfish released is most unlikely to be lower than 2·6 in. and will certainly be no more than 2·75 in.

Evidence for rate of growth is provided by those undersized white crayfish marked in the Carnac Island area in 1954 which were recaptured in the same area in December 1955 and December 1956. The 61 recaptured as whites in 1955 ranged in size from 2·75 to 3·45 in., with a mean of 3·03 in. The three whites recaptured in 1956 averaged 3·32 in. in carapace length (Table 2). Thus, from animals released as undersize in 1954, no undersized animals were recaptured in either 1955 or 1956, and this suggests that a comparison of the means is a valid method for obtaining growth rate.

Assuming the release mean of 1954 to be 2·70 in., the mean carapace length increment of the sexes combined was thus 0·33 in. for those recaptured in 1955, i.e. after 1 year's growth, and 0·62 in. for those recovered in 1956, i.e. after 2 year's growth. These recaptures of white crayfish, marked during 1954, in the seasons of 1955 and 1956 raise the question of the length of time an individual crayfish remains in the white phase. A complete answer cannot be given but in view of the immature nature of the crayfish in this phase it is simplest to assume that individuals reappear as whites only if they have not in the meantime attained maturity. From the length frequency distribution of the whites and the growth results it is unlikely that individuals would pass through more than three white phases before becoming mature.

IV. Conclusions

White crayfish occur regularly on the crayfish grounds of south-western Western Australia, being commercially exploited from late November to the end of December. They are recently moulted and immature and range in size from $2\frac{3}{8}$–$3\frac{3}{4}$ in. carapace length.

In the immediately premoult and newly moulted whites, no feeding occurs and hence crayfish in this condition are not taken in craypots. Premoult crayfish which are to become whites have a red shell covering the new white shell. At this stage they move towards, and accumulate in, shallow areas and, after moulting in mid November, tend to move offshore and disperse to feed in the deeper waters, and thus enter commercial craypots.

Data from recaptured marked white crayfish suggest that in the carapace length range 2·7–3 in. there is an average annual increase in size of about 0·3 in. It is suggested that the whites, which were recaptured after intervals of 1 and 2 years, failed to mature.

Marked, as well as penned, whites were observed as reds after periods of about 2 months. All this evidence points to the conclusion that whites are a pale-coloured phase in the life history of the Western Australian red crayfish *Panulirus longipes*.

If, in the future, the fishery for this species requires additional regulation, the white crayfishery should be limited or controlled since, in its operations, it takes considerable quantities of immature crayfish.

V. Acknowledgments

The following professional fishermen participated in the white crayfish tagging programmes and to each the author is grateful for willing cooperation and assistance: Messrs. J. Annear, Victor and Vincent Basile, F. Camarda, R. Hugel, F. Miragliotta, and Wilfred and William Poole. The assistance and companionship of Mr. J. Matthews during the underwater collections in the Geraldton area are also gratefully acknowledged.

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THE GASTROPOD GENUS *BEMBICIUM* PHILIPPI

By Hilda Anderson*

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Summary

A history of the nomenclature of the littorinid genus, *Bembicium* Philippi, 1846, and its characters are given, and the anatomy of species of the genus is discussed. Three species are recognized and redescribed: a reef-living species, *B. nanum* (Lamarck); an estuarine species, *B. auratum* (Quoy & Gaimard); and the species *B. melanostoma* (Gmelin) which normally inhabits sheltered bays and inlets.

Although all are intertidal animals, and show some measure of adaptability, each appears to be best suited to a particular habitat. *B. melanostoma* and *B. nanum* are usually found where the chlorinity of the water is close to that of the sea. *B. auratum* can withstand considerable variation in the chlorinity of its environment for periods of time which are not likely to be exceeded in its normal habitat. *B. melanostoma* mostly lives at higher tidal levels than *B. nanum*. In the aquarium *B. nanum* proved the most susceptible to desiccation.

The egg masses of *B. melanostoma* contain fewer and larger eggs than those of *B. auratum*. In the laboratory spawning of *B. auratum* occurred during the spring and early summer. Under the same conditions specimens of *B. melanostoma* deposited eggs in October. The differences between the eggs and their development, and between the times of spawning of the two species collected from different littoral regions are also discussed.

I. Introduction

This work arose from an investigation of the larval trematodes of *Bembicium* species, and the need to name the hosts of particular trematodes. This led to a full examination of the history of the genus *Bembicium* and of the species of this Australian genus. At the beginning of the work two species were recognized in South Australia: the striped open coast form with the stripes clearly showing in the outer part of the mouth, and the relatively tall, strongly sculptured estuarine form. The first was originally described by Lamarck as *Trochus nanus* and the second by Quoy and Gaimard as *Trochus auratus*. A third species, differing embryologically and conchologically from *B. auratum*, and anatomically and conchologically from *B. nanum*, is redescribed as *B. melanostoma* (Gmelin).

A representative collection of *Bembicium* specimens from south-western, southern, and eastern Australia has been examined. Although the size, shape, colouration, and sculpture of the shells of each species differs with habitat, differences within a local population are sometimes just as great as those between isolated populations. Further investigation of their anatomy, embryology, and breeding habits may show that some of those isolated populations deserve subspecific or even specific status but examination of the shells alone warrants the recognition of only three species.

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II. The Genus Bembicium

(a) *History of the Genus*

The first description of a *Bembicium* was that of Chemnitz (1781) who described a *Trochus in fauce nigerrimus* which was collected on one of Cook's voyages. The next description was that of Gmelin (1791) who briefly described the same species under the name *Trochus melanostomus*. Later authors continued to use the generic term *Trochus* for species of *Bembicium*. Lamarck (1822) described *Trochus nanus*. Quoy and Gaimard (1833, 1834) described four species (*Trochus nanus* Lamarck, *T. planus*, *T. auratus*, and *T. luteus*).

Gray (1839) described two species (*Littorina australis* and *L. imbricata*) which, he thought, would probably form with *T. melanostomus* Gmelin "a new section of the genus *Littorina*". He later placed them in a new genus, *Risella* (Gray 1840), but gave no definition of this genus.

Philippi, who apparently had not seen Gray's work, suggested (Philippi 1846) that the above named species were not trochids, and, although they might be closely related to the genus *Littorina*, the shape of their shells was sufficiently different to warrant the erection of a new genus. He, therefore, created the genus *Bembicium* and gave a generic description.

Later Gray (1847) again used the name *Risella* for the genus, and Philippi (1851) finding that Gray had named the genus in 1840 then adopted *Risella* as the generic term. The lack of description by Gray (1840) rendered *Risella* a nomen nudum; nevertheless for many years this name was used because Philippi (1851) had rejected his genus *Bembicium* as a synonym. An exception was provided by Tenison-Woods (1879) who suppressed the genus altogether, making it a species of *Littorina*—*L. melanostoma*. The name *Bembicium* has since been resurrected, and is now in current use (Iredale 1912).

(b) *Synonymy and Diagnosis of the Genus*

Genus BEMBICIUM Philippi, 1846

Trochus Chemnitz, 1781 (partim), p. 26. Gmelin, 1791 (partim), p. 3581. Lamarck, 1822 (partim), p. 30. Quoy and Gaimard, 1833 (partim), pl. 62; 1834 (partim), pp. 271, 273, 276. Deshayes and Edwards, 1839 (partim), pp. 555, 557; 1843 (partim), pp. 150, 157. Reeve, 1842*a* (partim), p. 185. Philippi, 1845 (partim), p. 66.

Littorina Gray, 1839 (partim), p. 141. Tenison-Woods, 1879 (partim), p. 64.

Risella Gray, 1840, p. 147; 1847, p. 150. Philippi, 1851, pp. 31, 39; 1853, p. 1. Adams and Adams, 1858, p. 318. Chenu, 1859, p. 302. Dunker, 1862, p. 42. Crosse, 1864, p. 225. Zelebor, 1866, p. 913. Angas, 1867, p. 209. Frauenfeld, 1868, p. 9. Tenison-Woods, 1876, p. 242. Kiener and Fischer, 1880, p. 462. Smith, 1884, p. 61. Tryon, 1887, p. 262. Pritchard and Gatliff, 1902, p. 92. Verco, 1908, p. 8. Hedley, 1909 (partim), p. 355.

Bembicium Philippi, 1846, p. 129. Iredale, 1912, p. 224; 1931, p. 208; 1936, p. 289. Hedley, 1916, p. 187; 1917, p. M51. May, 1921, p. 48. Musgrave, 1929, p. 344. Stephenson *et al.*, 1931, pp. 42, 61. Cotton and Godfrey, 1938, p. 10. Wenz, 1939, p. 523. Allan, 1950, p. 80. Macpherson and Chapple, 1951, p. 118. Dakin, 1952, p. 247. Kershaw, 1955, p. 307.

Diagnosis

Shell spiral, univalve, cyrtoconoid, imperforate, and non-nacreous; apex eccentric; 5–7 whorls, often eroded; sutures distinct, depressed, or indistinct; last

whorl acutely keeled, subangular, or rounded. Base flat, slightly concave or convex. External surface sculptured; whorls may be nodulose, crenated, or smooth; small shells usually more crenated than large shells; whorls marked by ridges and fine furrows parallel to sutures, and fine collabral growth lines; base marked by concentric ridges and spiral growth lines; usually, if ridges distinct, growth lines indistinct, if lines distinct, ridges indistinct; sometimes both distinct, sometimes both indistinct. Base usually paler than upper surface, with few or no dark flecks.

Interior smooth and polished. Aperture depressed, oblique, and a curvilinear triangle with convex sides; lip from columella to keel most convex, upper lip least curved; may be a shallow groove at margin of upper lip. Basal margin near columella thickened, polished, and sometimes reflected; in young specimens the reflection may form a distinct umbelicus. Columella and upper aperture paler than outer lip; the animal may give a grey tinge to the upper aperture. Basal margin almost smooth, faintly or distinctly crenated. Inner surface of base of aperture near keel thickened to form distinct or indistinct ridge. Operculum thin, oval, horny, translucent, paucispiral, and pale brownish yellow. Radula dentition 2.1.1.1.2.

(c) *General Anatomy*

Quoy and Gaimard described the colouration of parts of the animals, and noted that the sexes were separate. Kesteven (1902) briefly described the anatomy of a species which he called *Risella melanostoma* Gmelin. His description, and in particular his figure of the penis, shows that he was describing *B. nanum*. Other littorinids have been studied in greater detail. Linke (1933, 1935) described the reproductive systems of *Littorina littorea*, *L. rudis*, *L. obtusata*, and *Cremnoconchus syhadrensis*. Johansson (1939) described the anatomy and histology of the digestive, nervous, muscular, and circulatory systems of *L. littorea*, *L. obtusata*, and *L. rudis*, and later (1942) published an account of the crystalline style sacs of some littorinids.

In this investigation serial sections of *Bembicium auratum* were examined, and specimens of *B. auratum*, *B. melanostoma*, and *B. nanum* were dissected. It was found that there are few anatomical differences between (1) the three species of *Bembicium* and (2) the genera *Bembicium* and *Littorina*. The hypobranchial gland, the rudimentary crystalline style sac, the nephridium, and the digestive, circulatory, nervous, and muscular systems of the three species studied are essentially similar to those described by Johansson (1939, 1942) for *Littorina* spp. The osphradium which is simpler than that in *Littorina* was described by Kesteven (1902). Other sense organs are similar to those described by Johansson. The venous lacuna which, according to Kesteven, defines the dorsal and anterior distal part of the ctenidium was noticeable in some dissected specimens of *B. nanum* but in none of *B. auratum* or *B. melanostoma*.

Most diversity of structure between species and genera occurs in the reproductive systems. *Bembicium* spp. differ from *Littorina* spp. in the shape of the penis and the arrangement of the uterine glands; also *Bembicium* spp. have no penial glands, and have a closed vas deferens from the prostate to the penis. In *B. nanum* (as described by Kesteven) and *B. auratum* (Plate 1, Fig. 1) the seminal products pass through the penis and not along a groove in the side as in *Littorina*. The course of the vas deferens

in *B. melanostoma* appeared similar to that in *B. auratum* although it was not studied from sections. Except that the tubules of the gonad lie over those of the digestive gland and do not intertwine among them, the histology and structure of testis, vesicular seminalis, vas deferens to the prostate, and the prostate itself are similar to those described by Linke (1933) for *Littorina* spp.

The ovary of *Bembicium* is similar to that described by Linke for *L. obtusata* and *L. rudis* except that, like the testis, it lies over the digestive gland. It is a compact organ with the ovarian lobes grouped around the visceral arterial system. This

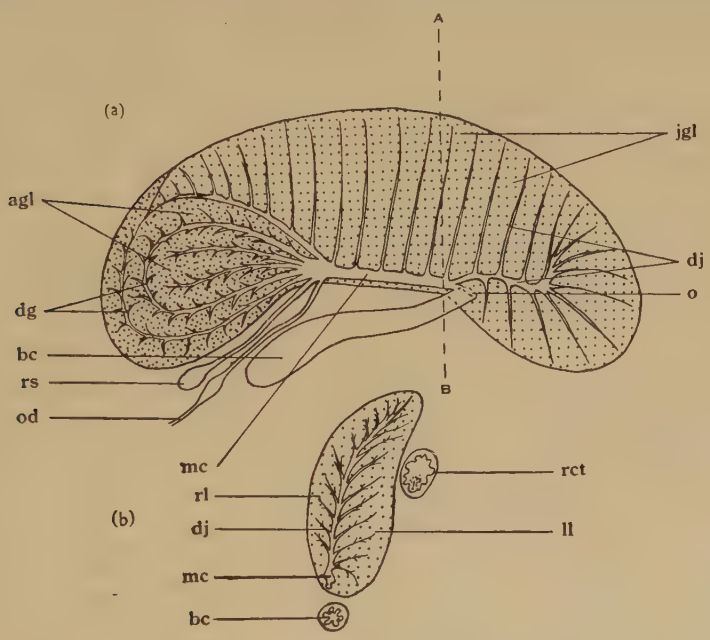

Fig. 1.—Diagrammatic representation of the uterus of *Bembicium auratum* seen (*a*) from the right, and (*b*) along line *A–B*. *agl*, albumen gland; *bc*, bursa copulatrix; *dg*, ducts of albumen gland; *dj*, ducts of jelly gland; *jgl*, jelly gland; *ll*, left lobe of jelly gland; *mc*, main cavity of uterus; *o*, opening of vagina; *od*, oviduct; *rct*, rectum; *rl*, right lobe of jelly gland; *rs*, receptaculum seminis.

arrangement could be seen only in young specimens in which the ovaries were still developing. The oviduct is short, and dips from the axial surface of the spire into the connective tissue under the kidney. It enters the mantle tissue below and to the right of the posterior part of the uterus where it forms a slight dilation; it narrows again before entering the uterus. The receptaculum seminis is a small bulb-like structure in the posterior part of the mantle between the oviduct and the uterus. Its muscular walls have internal folds like those described by Linke for *L. obtusata*. The duct from the receptaculum seminis enters the cavity of the uterus just behind the opening of the oviduct. The uterus is shown in Figure 1. No "capsule gland" was seen. The structure and histology of the glands appeared similar to that described by Linke for *Littorina* spp. The oviduct, the duct of the receptaculum seminis, and

the main ducts from the "albumen gland" enter the cavity of the uterus in the mid ventral region. Ducts from the "jelly gland" enter between this region and the short muscular vagina.

The bursa copulatrix is situated in the mantle tissue below the uterus. It enters the muscular vagina close to the opening into the mantle cavity. Its musculature and opening are similar to those described by Linke for *L. littorea*. The route taken by sperms from the bursa copulatrix to the receptaculum seminis is probably along a groove which was seen in the ventral wall of the main cavity of the uterus. Eggs were seen moving from the opening of the vagina to the ovipositor which is a light-coloured patch on the body to the right of the head in the same position as the penis in the male. The ovipositor has the form of two lobes which are the flattened ends of the edges of a groove running along the body from the vagina.

III. Bembicium Species

(a) *History of the Species*

The list of recorded species is as follows:

Trochus in fauce nigerrimus Chemnitz, 1781, Southern Ocean.
T. melanostomus Gmelin, 1791, Southern Ocean.
T. nanus Lamarck, 1822, southern Australia.
T. planus Quoy & Gaimard, 1833, 1834, Port Western, Bass Strait.
T. auratus Quoy & Gaimard, 1833, 1834, d'Entrecasteaux Channel, Tasmania.
T. luteus Quoy & Gaimard, 1833, 1834, King George Sound, Western Australia, and Port Western, Bass Strait.
Littorina australis Gray, 1839, Australia.
L. imbricata Gray, 1839, Australia.
T. melanostomus Reeve, 1842, Australia.
T. cicatricosus Jonas (Philippi, 1845), Australia.
Bembicium lividum Philippi, 1846, Australia.
B. vittatum Philippi, 1846, Adelaide, Australia.
B. pictum Philippi, 1846, Tasmania.
Risella flavescens Philippi, 1851, Norfolk Island.
R. plicatula Philippi, 1851, Norfolk Island.
R. grisea Phillippi, 1851, habitat unknown.
R. fimbriata Philippi, 1851, habitat unknown.
R. crassa Dunker, 1862, Sydney, Australia.
R. bruni Crosse, 1864, Spencer Gulf, South Australia.
R. kielmanseggi Zelebor, 1866, New Zealand (believed to be Botany Bay).
B. nodulosum Musgrave, 1929, Port Jackson.

When Philippi (1846) described the genus he listed eight species, two of which were new, and one of which he renamed (*B. pictum* = Quoy and Gaimard's *T. nanus* Lamarck). In 1851 he described four more species. Later (1853) he redescribed the 12 species he recognized. Adams and Adams (1858) cited seven and Chenu (1859) three species with no explanation for omitting the others. Crosse (1864) recognized nine species, one of which was new, but he was dubious of the validity of three of the species he included.

Tenison-Woods (1876) attempted to simplify the nomenclature. He thought that *R. bruni*, *R. livida*, *R. vittata*, and *R. imbricata* were varieties of a species, the male of which had been given the name *R. aurata*, and the female *R. nana*; *R.*

melanostoma was a synonym of *R. aurata*; and *R. plana* and *R. lutea* might constitute another species. Later (1879) he considered that they all constituted one species—*Littorina melanostoma*.

Smith (1884) considered that the genus *Risella* should be retained as distinct from *Littorina*, and, although he did not admit the validity of all the described species, he felt that some should be retained for "convenience" if only because of geographically distinct variations. Tryon (1887) again classified all the previously described species as *Risella melanostoma* (Gmelin), that being the earliest authentic name. Similarly Pritchard and Gatliff (1902) recognized only one Victorian species—*R. melanostoma* Gmelin; but they conceded that *R. nana*, *R. plana*, and *R. aurata* were varieties, *nana* being the most obvious.

Confusion still remains concerning the number of species in this genus, and the specific names used vary in different parts of Australia. Musgrave (1929) called the large mangrove form *Bembicium nodulosum*. Iredale (1931) also used the name "*B. nodulosum* (Gray)". Later Iredale (1936) eliminated this nonem nudum. Although Cotton and Godfrey (1938) cited six species, Cotton (personal communication) considers that some of these species are probably only varieties. Allan (1950) and Dakin (1952) recognize two species.

At present the name *B. melanostoma* (Gmelin) is used in New South Wales and Queensland for the open coast species with stripes clearly showing on the outer lip (Allan 1950; Dakin 1952); in Victoria, Tasmania, and South Australia this species is referred to as *B. nanum* (Pritchard and Gatliff 1902; May 1921, 1923; J. Hope Macpherson and B. C. Cotton, personal communications). In New South Wales and Queensland the nodulose, mangrove or estuarine species is known as *B. kielmanseggi* (Zelebor) (Iredale 1936; Allan 1950; Dakin 1952); in South Australia it has been known as *B. imbricatum* (Gray) (B. C. Cotton, personal communication), and in Victoria as *B. auratum* = *luteum* (Quoy & Gaimard) (J. Hope Macpherson, personal communication). A third species, which normally inhabits sheltered regions, is recognized in Victoria, Tasmania, and South Australia and known as *B. melanostoma* (Gmelin) (Pritchard and Gatliff 1902; May 1921, 1923; J. Hope Macpherson and B. C. Cotton, personal communications).

In this paper three species are recognized; the striped open coast species which is called *B. nanum* (Lamarck); the nodulose, estuarine species which is called *B. auratum* (Quoy & Gaimard); and the species which inhabits sheltered bays is called *B. melanostoma* (Gmelin). The synonymy and reasons for this classification are set out in the sections on individual species.

(*b*) *Taxonomic Characters*

(i) *Eggs*.—Specimens of *Bembicium* collected from Port Adelaide, Outer Harbour, South Australia, were separated into two groups on conchological differences, and put into separate aquarium tanks in the laboratory. Specimens in group A, which were identified as *B. auratum*, ranged in height between 11·2 and 15·1 mm. Specimens in Group B (identified as *B. melanostoma*) ranged in height between 2·5 and 10 mm. The anatomy of the two groups showed only minor differences, e.g. shape of penis.

Neither group was considered a variety of *B. nanum* because of distinct anatomical as well as conchological differences.

Group A produced egg masses similar to those produced by specimens of *B. auratum* collected from a different locality; these egg masses differed markedly from those laid by Group B in shape, in size of the eggs and their hyaline envelopes, and in the number of eggs contained in the masses. Frequency distributions of the diameter of the eggs, and the length and width of the hyaline envelopes were plotted (Fig. 2). The resulting histograms are bimodal, indicating that the eggs were produced by two different species.

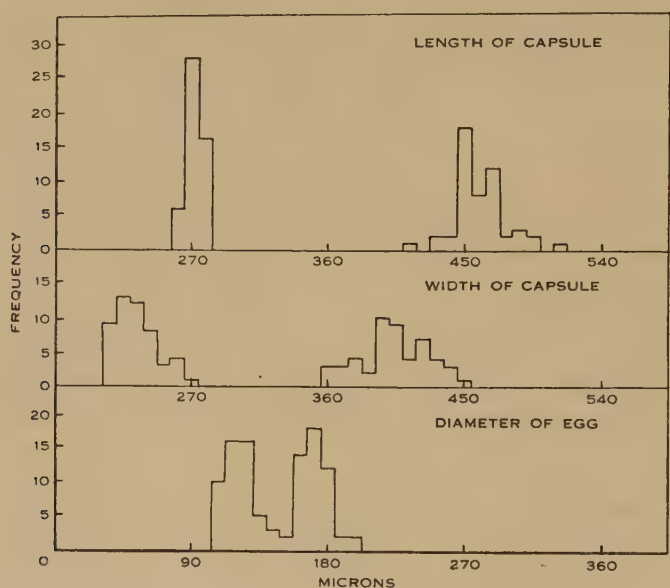

Fig. 2.—Frequency distribution of the length of egg capsules, width of egg capsules, and the diameter of the eggs of Group A (left) and Group B (right). Group A was *Bembicium auratum* and Group B was *B. melanostoma*.

In South Australia spawning of *B. auratum* probably occurs in the spring, because egg masses were deposited by this species between July and January when the animals were kept in the laboratory aquarium.

Specimens of *B. melanostoma* deposited egg masses in October. Although they were kept for 2 months after collection on October 8, 1952, egg masses were deposited only during the first 2 weeks in the aquarium. It is possible that *B. melanostoma* has either an earlier or a shorter spawning period than *B. auratum*.

The eggs and envelopes of *B. melanostoma* were larger than those of *B. auratum*, and their egg masses contained between 8 and 30 eggs, whereas those of *B. auratum* contained a hundred or more eggs (Plate 1, Figs. 2 and 3).

That *B. melanostoma* has no free-swimming veliger stage was seen when eggs kept in the aquarium developed past the veliger stage while still in the capsule.

However, they did not hatch. The embryos of *B. auratum* in the laboratory did not leave the capsules either, but they did not develop past the veliger stage. No egg masses of *B. nanum* were seen so it is not known how or when the embryos develop in this species.

(ii) *Analysis of Shell Shape.*—The ratios of height to width (H/W) of shells of about 1600 *Bembicium* specimens from seven localities in South Australia were calculated. Means of H/W in three populations of *B. nanum* were 0·47, 0·52, and 0·57 (505 specimens); in four populations of *B. melanostoma* means were 0·72, 0·73, 0·76, and 0·82 (622 specimens); in two populations of *B. auratum* both means were 0·96 (474 specimens). About 80 per cent. of a mixture of these populations of *B. auratum* and *B. nanum* could be correctly classified using H/W, but specimens of *B. melanostoma*, which had a mean H/W between the ratios of *B. auratum* and *B. nanum* could not be satisfactorily distinguished by this method. The histogram of H/W of the three species was broad, flat-topped, and unimodal.

A statistical analysis of the height and width measurements was made, and a very definite linear relationship was found to exist between height and H/W in all the samples studied. A derived relationship showed that the shells are a pointed arch shape in vertical section. This was verified by comparing the shells with the diagram obtained by plotting this derived relationship.

The analysis also showed such a large intraspecific variation between samples from different localities that statistically the shape of the shell is not a useful guide in discriminating species for the samples of *Bembicium* spp. examined.

(*c*) *Species*

Bembicium melanostoma (Gmelin, 1791)

Plate 2, Fig. 1; Plates 3–5(*a*, *b*, *c*)

Trochus in fauce nigerrimus Chemnitz, 1781, p. 26, pl. 161, figs. 1526*a*, 1526*b*.

Trochus melanostomus Gmelin, 1791, p. 3581. Deshayes and Edwards, 1839, p. 557; 1843, p. 157.

Trochus luteus Quoy & Gaimard, 1833, pl. 62, figs. 8–11; 1834, p. 271.

Trochus melanostomus Reeve, 1842*a*, p. 185; 1842*b*, pl. 218, fig. 16. Smith, 1884, p. 62.

Trochus cicatricosus Jonas, Philippi, 1845, p. 66, *Trochus* pl. 2, fig. 2.

Bembicium melanostona Philippi, 1846, p. 130. Hedley, 1916, p. 187; 1917, p. M51. May, 1921, p. 48; 1923, pl. 22, fig. 20. Stephenson *et al.*, 1931, pp. 42, 61. Cotton and Godfrey, 1938, p. 10. Wenz, 1939, p. 523. Macpherson and Chapple, 1951, p. 118. Kershaw, 1955, p. 307.

Bembicium luteum Philippi, 1846, p. 132.

Bembicium vittatum Philippi, 1846, p. 131. Cotton and Godfrey, 1938, p. 10.

Bembicium lividum Phillippi, 1846, p. 131.

Risella flavescens Philippi, 1851, p. 39; 1853, p. 7, pl. 2.8.1, figs. 17, 18. Smith, 1884, p. 62.

Risella plicatula Philippi, 1851, p. 39; 1853, p. 9, pl. 2.8.1, figs. 23, 24. Smith, 1884, p. 62.

Risella fimbriata Philippi, 1851, p. 31; 1853, p. 5, pl. 2.8.1, figs. 9, 10. Smith, 1884, p. 62.

Risella melanostoma Philippi, 1853, p. 8, pl. 2.8.1, figs. 21, 22. Adams and Adams, 1858, vol. 1, p. 318, vol. 3, pl. 33, figs. 5*a*–5*c*. Chenu, 1859, p. 302, fig. 2127. Crosse, 1864, p. 229, pl. 11, fig. 1. Tenison-Woods, 1876, p. 243. Smith, 1884, p. 61. Tryon, 1887 (partim), p. 262, pls. 49, 50. Pritchard and Gatliff, 1902 (partim), p. 92. Verco, 1908, p. 8. Hedley, 1909 (partim), p. 355.

Risella lutea Philippi, 1853, p. 4, pl. 2.8.1, figs. 1, 2. Chenu, 1859, p. 302, fig. 2126. Crosse, 1864, p. 237. Kiener and Fischer, 1880, p. 463, pl. 38, figs. 2, 2*a*, 2*b*. Smith, 1884 (partim), p. 61.

Risella vittata Philippi, 1853, p. 9, pl. 2.8.1, figs. 25, 26. Adams and Adams, 1858, p. 318. Crosse, 1864, p. 241. Tenison-Woods, 1876, p. 244.

Risella livida Philippi, 1853, p. 10, pl. 2.8.1, figs. 27, 28. Adams and Adams, 1858, p. 318. Crosse, 1864, p. 240. Tenison-Woods, 1876, p. 244.

Risella crassa Dunker, 1862, p. 42. Smith, 1884, p. 62.

Risella bruni Crosse, 1864, p. 239, pl. 11, fig. 3. Tenison-Woods, 1876, p. 244. Smith, 1884, p. 61.

Risella aurata Tenison-Woods, 1876, p. 243.

Littorina melanostoma Tenison-Woods, 1879 (partim), p. 64.

Bembicium bruni Cotton & Godfrey, 1938, p. 10.

Specimens Examined

QUEENSLAND: 107 specimens from 6 localities (northernmost locality: Low Isles). NEW SOUTH WALES: 11 specimens from 2 localities. VICTORIA: 30 specimens from 6 localities. BASS STRAIT: 21 specimens from 4 localities. TASMANIA: 19 specimens from 2 localities. SOUTH AUSTRALIA: 1358 specimens from 14 localities. WESTERN AUSTRALIA: 8 specimens from 2 localities (northernmost locality: Rottnest Island).*

Description

Neotype.—Shell cyrtoconoid; 6 whorls; sutures of lower whorls distinct; lower margin of whorls 4 and 5 weakly crenated, and projecting over those below; whorls flat, acutely carinate at lower margin; last whorl subangular, weakly crenated and marked by oblique, collabral, growth lines. Apex eroded, grey brown; lower whorls pale greenish grey-brown; last whorl mottled with greenish grey, grey, and brown.

Base flat, with faint growth lines and 4 indistinct concentric ridges; dirty greenish cream. Outer lip of aperture very dark brown with narrow, wavy, cream margin; upper aperture dull orange; columellar lip narrowly reflected, polished, and dull orange; remainder of basal margin faintly crenated. Height 12 mm. Width 13 mm.

Selected from a series from the W. L. May collection labelled "*Bembicium melanostoma* Gm." collected from the Furneaux Island Group.

General.—Shells usually small, thin, and elevated. If sutures distinct, upper whorls may be regularly crenated at lower margin which may project over lower whorls; if depressed, whorls rounded or flat. Last whorl usually rounded or subangular when whorls convex or sutures depressed, subangular or keeled when sides smooth, acutely keeled when crenated.

Colour combinations and patterns differ widely. May be muddy yellowish grey-brown, with darker brown flecks, especially on last whorl; yellowish grey on sutures and last whorl, dark brown on body of upper whorls; pale greenish grey-brown, with grey-brown apex, and flecks on last whorl; pale bluish grey, with grey-brown or brown markings and upper whorls; pale greyish brown, mottled or flecked

*A complete list of specimens, localities, dates of collection, and collector's names for each species may be obtained by application to the author.

with red-brown or yellow-brown; dark reddish brown, with yellowish brown flecks. Other combinations of these colours and patterns may occur.

Base rarely slightly convex; if flecked, flecks usually near keel and small.

Outer lip of aperture yellowish brown, brown, or almost black; usually evenly coloured but may have patches of dark brown shading into a lighter ground, or light patches on a dark ground. Columellar lip pale yellow, orange, or reddish brown; may be narrowly reflected. Upper part of aperture pale yellow, orange, or brown. Internal ridge near keel rarely pronounced.

Body $3\frac{1}{2}$–$4\frac{1}{2}$ whorls; visceral body whorl almost circular in transverse section; digestive gland normally black, testis orangy yellow, ovary pale bluish green, penis bulbous, with a deep ventral groove, and annulated stalk; when contracted, body and stalk of penis almost as broad as long.

Average diameter of eggs 172 μ (149–197 μ); average width of envelopes 404 μ (358–451 μ); average length of envelopes 460 μ (413–512 μ). Irregularly shaped egg masses contain between 8 and 30 eggs (Plate 1, Fig. 2).

Shells of *B. melanostoma* are distinguished from those of *B. auratum* and *B. nanum* chiefly by the colour, shape, and size, by the reflection and colour of the columellar region, and by the regular sculpture and crenation; however, it is sometimes difficult to distinguish between specimens of *B. auratum* and *B. melanostoma*; also *B. melanostoma* may be distinguished from *B. nanum* by the number and shape of the whorls forming the body of the animal itself, and by the shape of the penis, and from *B. auratum* by the size of the eggs and their hyaline envelopes, by the number of eggs in the egg masses, and by the shape of the egg masses.

Systematic Position

The first description by Chemnitz of *Trochus in fauce nigerrimus* was short, and his figures were very poor. Gmelin's description of *Trochus melanostomus* was equally short and inconclusive: "Trochus testa obtusa pyramidali virente maculata; apertura intus nigerrima". Despite this, by common consent, authors reviewing the genus have retained Gmelin's name to describe one or other species of the genus.

The original specimen described by Chemnitz was recorded as being "ex museo nostro". However, it could not be found among the specimens in the Chemnitz and Spengler collections (G. Thorson, personal communication).*

The holotype was collected on one of Cook's voyages in the South Seas, but Chemnitz gave neither date of collection, the collector's name, nor any details of the habitat. Cook made three voyages to the Pacific Ocean, on each of which he was accompanied by naturalists. On the first voyage (*Endeavour*, 1768–71) Banks and Solander collected at Botany Bay and various places in Queensland (Cook 1893). On the second voyage (1772–75) the *Adventure*, consort ship to Cook's *Resolution*, under the command of Captain Furneaux, anchored for some time in Adventure Bay, Tasmania (Cook 1777). On the third voyage (1776–80) Cook's ships also anchored

*These collections are housed at the Universitetets Zoologiske Museum, Copenhagen. During the first half of the 19th century many specimens from these collections were sent to different countries for exhibition, and not all were returned to Copenhagen. *Trochus in fauce nigerrimus* was apparently one of the specimens lost in this way.

in Adventure Bay (Cook 1784). Chemnitz' book was published in 1781, the year following the completion of Cook's third voyage. The holotype could have been collected on any one of these voyages, and the locality could be Botany Bay, Queensland, or Tasmania.

The number of localities from which the original specimen could have been collected, and the lack of adequate description, figures, and data on collection, made it necessary to redescribe *B. melanostoma*. The most helpful diagnostic statement in Gmelin's description was "apertura intus nigerrima". Therefore, the species which has been described as *B. melanostoma* is the one which is most often completely dark in the mouth region. The descriptions and figures of Philippi (1846, 1853) and of Crosse (1864) show that both authors came to the same conclusion. The first figures of *B. melanostoma* are those of Philippi (1853); Crosse's figure is similar although the colouration is slightly different.

The neotype was chosen because the lower margin of the larger whorls projects over the whorls below, it is small ("hardly attaining the size of a small hazel nut"), and has a dark aperture. These were the only features described by Chemnitz.

Deshayes and Edwards description of *T. melanostomus* could apply equally well to some specimens of *B. auratum* or *B. melanostoma*. This may explain why Philippi (1846) equated *B. auratum* and *B. melanostoma*, although his figure of *melanostoma* is quite unlike the figures of *auratum* by either Quoy and Gaimard or Kiener and Fischer.

The use in Victoria of the names *B. auratum* and *B. luteum* as synonyms requires discussion. The original description and figures of *B. luteum* (Quoy and Gaimard 1833, 1834), and the photographs of the original specimen (Plate 2, Fig. 2(*c*)) are suggestive of specimens of *B. melanostoma* from the Port Adelaide River. Many of their specimens were collected in estuaries. Quoy and Gaimard discuss, but do not figure, a large "variety" which was present in the same habitat. That situation is similar to the one at Outer Harbour, South Australia, where specimens of *B. melanostoma* and *B. auratum* were found together. It is probable that their large "variety" was *B. auratum*. Philippi's (1853) figures 1 and 2 of *R. lutea* resemble some specimens of *B. melanostoma* collected from the Port Adelaide River. His figure 3, which he labelled "*R. lutea* var.?" is Quoy and Gaimard's figure 19 of *R. aurata*. This confusion could also account for the similarity between Tryon's figure 6 labelled *R. lutea* (Tryon 1887) and specimens of *B. auratum*.

Crosse (1864) described both *R. aurata* and *R. lutea* in detail. He mentioned that the mouth aperture of *R. aurata* was yellowish white, more or less spotted with brown, whereas the aperture of *R. lutea* was of a uniform yellowish tone. Crosse considered that *R. lutea* was a smaller, perfectly distinct species with differences from *R. aurata* in the region of the aperture, and in colouration. His descriptions of both *R. lutea* and *R. bruni* could be applied to some forms of *B. melanostoma*. Crosse also recommended Kiener's drawings of *R. lutea*.

Kiener's figures of *R. aurata* and *R. lutea* are of quite distinct forms (Kiener and Fischer 1880). His figure 2 of *R. aurata* is like Quoy and Gaimard's figure 19, and both figures 2 and 2*a* are very like some shells classified as *B. auratum*. Kiener's figures 2 and 2*a* of *R. lutea* are like some specimens of *B. melanostoma*; figure 2*b* is

like other specimens of *B. melanostoma*. Fischer described *R. aurata* as having two rows of nodules on the whorls and a chestnut-coloured and spotted mouth; of *R. lutea* he said that the aperture may be brown or yellowish but he did not mention spots. He also described the basal border of the aperture of *R. lutea* as being "pleated". This pleating has not been seen in any specimens assigned to the species *B. auratum*.

It has, therefore, been concluded that *B. luteum* is synonymous with *B. melanostoma* and not with *B. auratum*.

The form described by Philippi (1851, 1853) as *R. fimbriata* had a very depressed shell. In Victoria *B. fimbriatum* is considered synonymous with *B. planum* (J. Hope Macpherson, personal communication), but, according to Philippi, it differed from *B. planum* in having deeper, transverse furrows, an umbilical crevice, a dark brown aperture, and more prominent keel. Specimens most like Philippi's description and figures were some *B. melanostoma* from Salt Creek Causeway, Yorke Peninsula. Although these shells are not as depressed as that represented in Philippi's figures they show the features which he particularly referred to in his description of *R. fimbriata*, and they also have a bluish colouration similar to his figure. It seems likely that the shell Philippi called *R. fimbriata* was a specimen of *B. melanostoma*. A specimen from King Island which was selected by Iredale (personal communication) as a typical specimen of *B. flavescens* (Philippi) was also very similar to some specimens of *B. melanostoma*. This specimen formed part of a collection of *Bembicium* spp. examined at the Australian Museum, Sydney.

From the short description and rather poor figure of the shell which Reeve (1842*a*, 1842*b*) called *Trochus melanostomus* it seems probable that he was describing a *fimbriatum*-like *B. melanostoma*.

Philippi's descriptions and figures suggest that the names *B. vittatum*, *B. lividum*, and *R. plicatula* are synonymous with *B. melanostoma*.

Dunker (1862) described *B. crassa* from very thick, whitish shells, marked by a few brownish yellow flecks on the more yellowish upper whorls. The aperture and columella were brownish yellow, and the outer border was white. Specimens bearing the closest resemblance to this description were from Coral Point, near Sarina, Queensland. They were not dissected but the shape of their shells was most like other Queensland specimens classified as *B. melanostoma*. Many of these were lighter-coloured, with thicker shells, than southern specimens. Small specimens were usually darker than large ones, and the shells were thinner. The aperture of large specimens varied from creamy white to light brown, but two small specimens from Coral Point had dark brown apertures. Some had a few dark blotches on the outer lip of the aperture. The base and upper part of the shell was creamy white, creamy white mottled with light brown, light brown mottled with cream, or light brown. Large shells usually showed a marked ridge on the base of the throat.

A study of the anatomy and embryology of these northern specimens may show that they constitute another species or subspecies. However, because the shape and colour of the shells examined were more like southern specimens of *B. melanostoma* than specimens of *B. nanum* or *B. auratum* they have been classified as *B. melanostoma*.

Habitat

B. melanostoma normally inhabits sheltered, rocky bays, mudflats, or mangrove swamps. In South Australia they were usually collected from regions where they would have to withstand long periods of desiccation between high tides, and the oxygen supply in the water would be less than that in water washing open coast reefs. They were found only where the chlorinity (see Sverdrup, Johnson, and Fleming 1942) closely approximated to that of sea-water. Their habitat was most thoroughly studied in the Port Adelaide River, which is a wide, shallow, muddy estuary receiving a little fresh water from drains and swamps near the coast. *B. melanostoma* was found on the mangroves which fringe the mouth of the estuary, on jetty piles, and on mud banks. The chlorinity of the water in the estuary varies little throughout the year. Between March and October 1948, and October 1950 and May 1951 the maximum chlorinity was 21·86‰, and the minimum was 19·43‰ (Chittleborough 1952).

Specimens from Queensland, Victoria, and Tasmania showed similar ecological preferences.

Holotype locality.—Southern Ocean.

Neotype.—D.14590, South Australian Museum, Adelaide.

Neotype locality.—Furneaux Island Group, Bass Strait.

Distribution.—South-western, southern, and eastern Australia.

Bembicium nanum (Lamarck, 1822)

Plates 3–5(*d*, *e*, *f*)

Trochus nanus Lamarck, 1822, p. 30. Quoy and Gaimard, 1833, pl. 62, figs. 5–7; 1834, p. 273. Deshayes and Edwards, 1839, p. 555; 1843, p. 150. Delessert, 1841, pl. 36, figs. 3*a*–3*c*.

Trochus planus Quoy & Gaimard, 1833, pl. 62, figs. 13, 14; 1834, p. 273.

Littorina australis Gray, 1839, p. 141.

Bembicium nanum Philippi, 1846, p. 131. May, 1921, p. 48; 1923, pl. 22, fig. 21. Cotton and Godfrey, 1938, p. 10. Macpherson and Chapple, 1951, p. 118. Kershaw, 1955, p. 307.

Bembicium planum Philippi, 1846, p. 131. Cotton and Godfrey, 1938, p. 10. Macpherson and Chapple, 1951, p. 118. Kershaw, 1955, p. 307.

Bembicium pictum Philippi, 1846, p. 132.

Risella grisea Philippi, 1851, p. 31; 1853, p. 8, pl. 2.8.1, figs. 19, 20. Smith, 1884, p. 62.

Risella nana Philippi, 1853, p. 6, pl. 2.8.1, figs. 13–16. Adams and Adams, 1858, p. 318. Chenu, 1859, p. 302, fig. 2125. Crosse, 1864, p. 234. Angas, 1867, p. 209. Tenison-Woods, 1876, p. 247. Smith, 1884, p. 61. Verco, 1908, p. 8.

Risella plana Philippi, 1853, p. 5, pl. 2.8.1, figs. 6, 7. Adams and Adams, 1858, p. 318. Crosse, 1864, p. 236, pl. 11, fig. 2. Angas, 1867, p. 209. Tenison-Woods, 1876, p. 248. Verco, 1908, p. 8.

Risella picta Philippi, 1853, p. 6, pl. 2.8.1, figs. 11, 12.

Littorina melanostoma Tenison-Woods, 1879 (partim), p. 64.

Risella melanostoma Tryon, 1887 (partim), p. 262, pl. 49. Pritchard and Gatliff, 1902 (partim), p. 92.

Bembicium melanostoma Allan, 1950, p. 81, pl. 19, fig. 4. Dakin, 1952, p. 247, pl. 61, fig. 7.

Specimens Examined

QUEENSLAND: 59 specimens from 9 localities (northernmost locality: Bowen Harbour). NEW SOUTH WALES: 116 specimens from 4 localities. VICTORIA: 54 specimens from 12 localities.

BASS STRAIT: 7 specimens from 2 localities. TASMANIA: 107 specimens from 6 localities. SOUTH AUSTRALIA: 568 specimens from 9 localities (westernmost locality: Corny Point beach).

Description

Shells depressed, usually thick, some more than 2 mm thick at base. If sutures indistinct, both upper and lower margins of whorls smooth or slightly crenated; if distinct, crenations usually larger and more regular on lower than upper margin, and upper whorl may project over lower; if sutures depressed, sides of shell usually smooth with convex whorls; distinctly crenated shells may have concave whorls; crenations may occupy positions on adjacent whorls so that ridges radiate from apex to keel. Last whorl rarely rounded.

Whorls marked by regular, dark, oblique stripes approximately at right angles to growth lines; distribution, depth of colour, and distinctness of stripes vary. Stripes may be present near aperture, on last whorl, on last and higher whorls, or barely distinguishable; may be pale or dark grey, brownish red, brown, or almost black on a ground colour of yellowish white, grey, or pale yellowish brown; usually as wide as distance between them.

Base rarely slightly convex; may have flecks of dark colour on keel, or on keel and ridges; those on keel a continuation of stripes on last whorl. Outer lip of aperture creamy white, pale yellowish orange, or pale orangy brown, usually spotted or striped with dark pigment continuous through shell which may be thinner where pigmented; stripes may be covered by enamel of interior. Upper aperture creamy or pale orange; columellar lip cream, pale creamy orange, or orange. Internal ridge near keel distinct in large shells, less so in smaller shells.

Body $2\frac{1}{2}$–$3\frac{1}{2}$ whorls; visceral body whorl a dorsoventrally flattened ellipse in transverse section; digestive gland normally greenish brown; testis yellowish green to yellowish brown; ovary pale grey, green, pink, or grey-green; penis annulated and dorsoventrally flattened, with a short stalk (Kesteven 1902).

The bodies of specimens of *B. nanum* differ from those of *B. melanostoma* and *B. auratum* in the number and shape of the body whorls, and in the shape of the penis. The shells are distinguished from those of *B. melanostoma* and *B. auratum* by the stripes on the upper whorls and on the outer margin of the aperture, by the shape, the thickness of the shell, and the pronounced ridge on the interior of the aperture.

Systematic Position

This species has sometimes been called *B. melanostoma* (Allan 1950; Dakin 1952). The shells are rarely dark in the interior of the mouth, and are unlikely to be the species which Gmelin described. Neither do they fit the descriptions of *melanostoma* by Deshayes and Edwards, Philippi, or Crosse. On the other hand, the descriptions of *Trochus nanus* by Lamarck, Deshayes and Edwards, and Quoy and Gaimard, as well as the figures of Delessert and Quoy and Gaimard clearly refer to this open-coast, striped form.

B. planum is considered a synonym of *B. nanum* for the following reasons. The original description of *planum* was of a very flattened, acutely keeled shell with

reddish brown striations on the whorls, and on the external border of the aperture. Quoy and Gaimard, whose figures of *T. planus* are poor, considered that the colouration was very similar to that of *B. nanum*. *B. planum* was next described by Philippi (1846, 1853) as a depressed cone, fairly thin-shelled, brownish white, sometimes with indistinct, oblique, brown lines, with flat whorls, and a white aperture. Crosse also described and figured *B. planum*. He said it was the most flattened species, and that the brown markings were only present in young specimens, disappearing in the adults. He described the aperture as mainly white with several small, brown flecks near the external border, and the columella and neighbouring parts as pale orange.

Many specimens of *Bembicium* collected from rocky regions answer these descriptions. Specimens collected from one locality sometimes form a continuous range from the form described above to typical specimens of *B. nanum*, and dissections showed that the anatomy of *B. planum* is similar to that of *B. nanum*.

Philippi's descriptions and figures suggest that the names *B. pictum* and *R. grisea* are also synonyms of *B. nanum*. Gray's description of *Littorina australis* shows that he was describing a specimen of *B. nanum*. This was recognized by both Philippi and Crosse.

Habitat

B. nanum normally inhabits marine reefs or rocky beaches. None was found on mangroves. In South Australia, with the exception of three specimens collected from the Patawalonga Creek, this species was found where the chlorinity of the water varies very little, where the water is well oxygenated, and periods of desiccation between tides are usually short. Where *B. nanum* and *B. melanostoma* were collected together, *B. nanum* was found living lower down the beach than *B. melanostoma*. Aquarium experiments showed that of the three species, *B. nanum* was most sensitive to desiccation.

Their habitat was studied most thoroughly at Marino Rocks, which is a low rocky reef on the east side of Gulf St. Vincent, South Australia. In the mid-littoral regions of the beach are numerous, small, loose boulders on which *B. nanum* was found abundantly. Between December 1949 and April 1951 the chlorinity of the water washing this reef varied between 20·3‰ and 20·9‰ (Thomas and Edmonds 1956).

Specimens of *B. nanum* from Queensland, New South Wales, Victoria, and Tasmania showed similar ecological preferences (W. Stephenson and J. Hope Macpherson, personal communications).

Type.—Muséum d'Histoire Naturelle, Geneva.

Type locality.—Southern Australia.

Distribution.—Southern and eastern Australia.

Bembicium auratum (Quoy & Gaimard, 1834)

Plates 3–5 (*g*, *h*)

Trochus auratus Quoy & Gaimard, 1833, pl. 62, figs. 15–19; 1834, p. 276.
Littorina imbricata Gray, 1839, p. 141.
Bembicium imbricatum Philippi, 1846, p. 132. Cotton and Godfrey, 1938, p. 10.

Risella imbricata Philippi, 1853, p. 4, pl. 2.8.1, figs. 4, 5. Adams and Adams, 1858, p. 318. Crosse, 1864, p. 242. Tenison-Woods, 1876, p. 244. Smith, 1884, p. 61.

Risella lutea Philippi, 1853, p. 4, pl. 2.8.1, fig. 3. Adams and Adams, 1858, p. 318, pl. 33, fig. 5. Angas, 1867, p. 209. Tenison-Woods, 1876, p. 248. Smith, 1884 (partim), p. 61.

Risella aurata Crosse, 1864, p. 233. Kiener and Fischer, 1880, p. 462, pl. 34, figs. 2, 2*a*. Smith, 1884, p. 62.

Risella kielmanseggi Zelebor, 1866, p. 913. Frauenfeld, 1868, p. 9, pl. 1, figs. 11*a*–11*e*.

Littorina melanostoma Tenison-Woods, 1879 (partim), p. 64.

Risella melanostoma Tryon, 1887, (partim), p. 262, pl. 49. Pritchard and Gatliff, 1902 (partim), p. 92.

Bembicium nodulosum Musgrave, 1929, p. 344. Iredale, 1931, p. 208.

Bembicium kielmanseggi Iredale, 1936, p. 289. Allan, 1950, p. 81, pl. 19, fig. 5. Dakin, 1952, p. 248, pl. 61, fig. 5.

Bembicium auratum Macpherson & Chapple, 1951, p. 118.

Specimens Examined

QUEENSLAND: 56 specimens from 5 localities (northernmost locality: Bingham, near Bundaberg). NEW SOUTH WALES: 35 specimens from 2 localities. VICTORIA: 33 specimens from 6 localities. TASMANIA: 12 specimens from 2 localities. SOUTH AUSTRALIA: 573 specimens from 5 localities. WESTERN AUSTRALIA: 14 specimens from 3 localities (westernmost locality: Cockburn Sound, Fremantle).

Description

Shells large, elevated, and thin. Sutures rarely distinct. Surface may be smooth or show nodulose protuberances, especially along base of each whorl; nodules may be large and may occupy similar positions on adjacent whorls so that there are rows of nodules from apex to keel. Last whorl rarely rounded.

Colour combinations and patterns vary; may be dark greyish brown irregularly marked with yellowish grey flecks, or with both yellowish grey and dark brown flecks; very pale grey near sutures, dark brown on rest of whorls, except last which is mottled with dark and light patches; greyish white with irregular dark patches on all whorls, or dark brown with patches of pale grey.

Base rarely slightly concave; patches of colour usually small and on growth lines.

Outer lip of aperture varies from pale greyish yellow to brown, very often mottled; columella lip usually pale yellowish grey, but may be pale yellowish brown; upper part of aperture varies from light yellowish grey to greyish brown. Internal ridge near keel not distinct.

Body $3\frac{1}{2}$–$4\frac{1}{2}$ whorls; visceral body whorl almost circular in transverse section; digestive gland usually brown; testis orangy yellow to orangy brown; ovary pale fawn, pale green, pale pink, or pale khaki-green; penis bulbous, with deep ventral groove and annulated stalk. Both stalk and body of penis are longer relative to their width than those of *B. melanostoma*.

Average diameter of eggs 122 μ (105–147 μ); average width of envelopes 234 μ (215–273 μ); average length of envelopes 272 μ (258–279 μ). Bean-shaped egg masses contain over 100 eggs (Plate 1, Fig. 3).

B. auratum may be distinguished from *B. melanostoma* and *B. nanum* chiefly by the greater height relative to the width and by the nodulose appearance and colour

of the shell; from *B. nanum* by the number and shape of the whorls forming the body of the animal, and by the shape of the penis; and from *B. melanostoma* by the size of the eggs and their hyaline envelopes, by the shape of the egg masses, and by the greater number of eggs in each mass.

Systematic Position

The description of *B. auratum* by Quoy and Gaimard (1834) is not very detailed. However, two sentences in their description "Les tours de spire sont serrés, à peine distincts, rugueux, ondulés, formant des sortes de plis grossiers en long", and "L'ouverture est large . . . maculée de brun en dedans" seem to apply to the species described here. Although Quoy and Gaimard's figures 15 and 16 of *B. auratum* are not good, figure 19 is very similar to many specimens examined. The more detailed descriptions of *B. auratum* by Crosse, and Kiener and Fischer, as well as Kiener's figures support the conclusion that *B. auratum* (Quoy & Gaimard) is the correct name for the large, nodulose, grey-brown species of *Bembicium*. And the photographs of the original specimens (Plate 2, Figs. 2(*a*) and 2(*b*)) provide conclusive evidence that this is the correct name for this species.

Some of Kiener and Fischer's specimens came from "Holfast Bay" (i.e. Glenelg, South Australia). The only abundant species at Glenelg lives in the Patawalonga Creek. These shells are similar to the ones they described as *R. aurata*, and to the photographs of Quoy and Gaimard's original specimen. Therefore, they have been classified as *B. auratum*.

The first figure of *Bembicium imbricatum* (Gray) was that of Philippi in 1853. He depicted a very worn, nodulose shell of a type more like *B. auratum* than any other described species. Some worn specimens of *B. auratum* resemble this figure. Although Zelebor gave the locality of *R. kielmanseggi* as New Zealand, no *Bembicium* species has since been collected in New Zealand. As members of the Novara Expedition collected at Botany Bay, and Frauenfeld's figures depict the nodulose, mangrove *Bembicium* found in New South Wales, Botany Bay is accepted as the habitat of *B. kielmanseggi*. Shells of *Bembicium* collected from mangrove, muddy, or estuarine regions in Queensland, New South Wales, Victoria, and Tasmania are similar to some collected in similar regions in South Australia, and indicate that they all belong to one species. The animals have been examined only in specimens from South Australia, New South Wales, and Queensland. Their anatomy and body colouration also supported this conclusion. A description of the egg masses of *B. kielmanseggi* (L. Woolacott, personal communication) in New South Wales also applies to those produced by *B. auratum* from South Australia, suggesting an analogy of egg masses.

It would thus appear that *B. imbricatum* (Gray) and *B. kielmanseggi* (Zelebor) are synonyms of *B. auratum* (Quoy & Gaimard).

Habitat

In South Australia specimens of *B. auratum* were found chiefly in estuaries and on mangroves. A very few were found on a marine reef. Specimens from other states also showed a preference for mangrove regions, estuaries, and sheltered rocky bays or inlets. Large numbers were collected from the Patawalonga Creek, which is a small, tidal estuary receiving fresh water from several intermittent streams.

A depression in the creek bed near the mouth forms a long, narrow pool at low tide. The bottom is formed of mud, a little sand, and dead and decaying "gulfweed", which is composed chiefly of *Posidonea* with some *Cymodocea* and *Zostera*. Mixed with this soft stratum are rocks, old tins, bottles, and other rubbish from which many specimens of *B. auratum* were collected.

The upper and lower limits of their distribution in the creek were such that they would have to withstand long periods of either desiccation or immersion. Some specimens of *B. auratum* survived for 3 months out of water. Because of the large amount of decaying vegetable matter the oxygen supply in the pool would probably be less than that of most other habitats in which members of this genus were found.

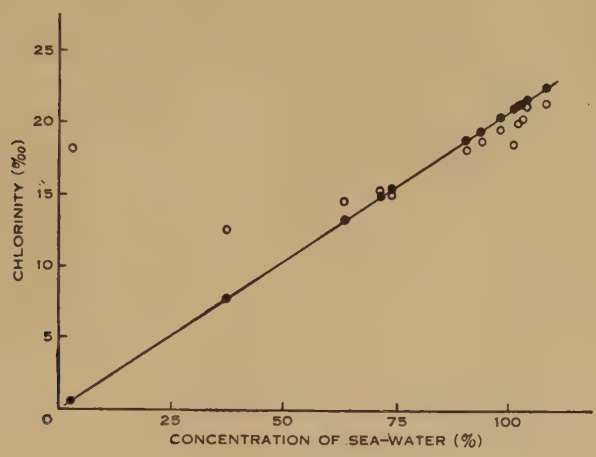

Fig. 3.—The relationship between the chlorinity of the internal and external media following the immersion for two days of *Bembicium auratum* in different external media. Each circle represents a determination made on the fluid obtained from 20 individuals. ○, internal medium; ●, external medium.

Their food, as judged by an examination of stomach contents, consists of dead or decaying vegetation, unicellular plants and animals, algal spores, and probably bacteria.

The chlorinity of the water in the Patawalonga Creek varies considerably throughout the year. Between March and December 1950 the maximum chlorinity recorded was 21·8‰, and the minimum was 0·5‰.

Experiments were carried out on groups of 20 specimens of *B. auratum* of similar size, to examine the relation of chlorinity (using the method of Van Slyke (1923)) and freezing point depression (using a Beckmann thermometer) between the internal and external media. Sufficient blood could not be collected from the heart or anterior sinus so it was taken from the visceral sinus behind the nephridium; although this fluid was coloured by haemocyanin it also contained fluid from the nephridium. To obtain sufficient volume for the two determinations it was diluted by adding an equal volume of redistilled water; corrections were made for this dilution.

When the animals were completely immersed for 2 days in concentrations of seawater with a chlorinity greater than 15·0 the chlorinity of the blood plus kidney fluid was less than that of the external medium. In concentrations of sea-water with a chlorinity less than 15·0 the chlorinity of the internal medium was greater than that of the external medium. In all experiments, the depression of freezing point of the internal medium ($\triangle_i$) was greater than that of the external medium ($\triangle_o$).

Figures 3 and 4 show a change in the body fluids at a dilution of approximately 70 per cent. (i.e. 15·0‰ Cl) sea-water, when the internal medium was also about 70 per cent. of its normal concentration. In sea-water concentrations of between 70 and

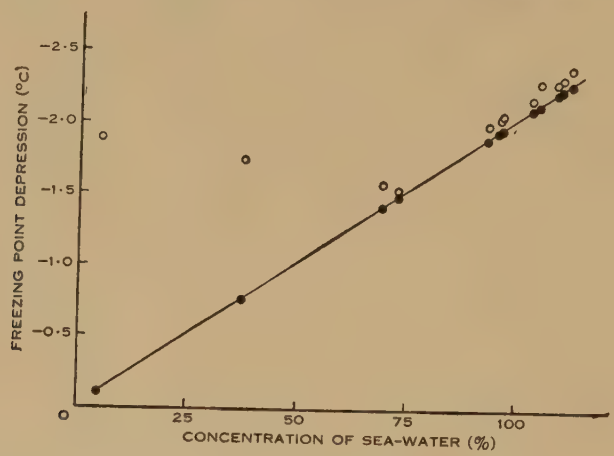

Fig. 4.—The relationship between the freezing point depressions of the internal medium ($\triangle_i$) and the external medium ($\triangle_o$) following the immersion for two days of *B. auratum* in different external media. Each circle represents a determination made on the fluid obtained from 20 individuals. ○, internal medium; ●, external medium.

100 per cent. the animals moved about readily. As the concentration of sea-water was decreased from 70 to 35 per cent. the period of activity lessened rapidly; below 35 per cent. the animals closed their opercula very soon after immersion. Although the operculum may not completely seal the animal from contact with the external medium, the small amount of salt and water exchange which would occur could be withstood by the animal for short periods. When the animals were immersed in water with 0·6‰ Cl the chlorinity of the internal medium fell from approximately 21·0 to 18·2. That they would rarely be subjected to such a dilute medium for 2 days was shown by an examination of chlorinity in the Patawalonga Creek. Under circumstances where the fluctuations would be expected to be at a maximum, the lowest chlorinity recorded was 3·9; the highest, 19·0, occurred at high tide 4 hours later.

It appears, therefore, that specimens of *B. auratum* are able to withstand considerable dilution of their external medium for periods which are not likely to be exceeded in their normal habitat. The protection afforded by the shell and operculum was shown to be important in this process.

Type.—In Muséum National d'Histoire Naturelle, Paris.

Type locality.—D'Entrecasteaux Channel, Tasmania.

Distribution.—South-western, southern, and eastern Australia.

IV. Discussion

A taxonomic examination of *Bembicium* spp. requires that large numbers of specimens should be examined. Many varieties of *Bembicium* spp. have been given specific status because too much significance was given to individual variations in the shape and colouration of the shells. It is rarely possible to distinguish one species from another on one characteristic only. Each shell must be considered in relation to a number of characteristics, all of which are variable. In this investigation the anatomy and embryology of the animals, as well as the conchology, were examined, with the result that three species have been recognized. However, some specimens from Queensland may constitute a subspecies or species.

It was thought that the height–width ratio of the shells could be used to discriminate species, but the differences in shape of specimens of one species collected at different localities were sometimes greater than the differences between species. Also, in large samples of a species collected from one locality, the intraspecific variations from the mean height–width ratio were very large.

Differences in the colouration of both the interior and exterior of the shell, differences in the columella lip, in the size and shape of the shell, and in the habitat are important in the identification of species.

The distribution of *Bembicium* spp. showed that these animals possess some adaptability to different environments. *B. nanum* normally inhabits marine, rocky regions, and no specimen was found on mangroves; however, some specimens were found in the estuarine Patawalonga Creek. *B. melanostoma* was found on mangroves, on mud flats and in sheltered, marine, rocky regions, but not where the chlorinity changes were great. *B. auratum* seems the most adaptable to chlorinity changes. This species was collected mostly from estuarine or mangrove regions, but some were found on reefs.

The modes of development of species of *Bembicium* may be related to the conditions under which they live. *B. melanostoma* normally lives high up the beach, and eggs laid in late winter are less likely to be desiccated than eggs laid later in spring. The necessity for eggs to develop before late spring or summer does not arise with *B. auratum*, which inhabits the Patawalonga pool. The size of the eggs and hyaline envelopes may also be associated with the normal habitat of the species. Animals which live in the spray zone of the beach are normally viviparous, e.g. *Littorina saxatilis* (*rudis*) (Linke 1933), or have the veliger stage suppressed. Those which live in tidal rock pools frequently have planktonic eggs which develop into free swimming veliger larvae, e.g. *L. littorea*. *L. neritoides*, which normally lives in the zone just below that occupied by *L. saxatilis*, is atypical in also having planktonic eggs which develop into free-swimming veliger larvae (Lebour 1935). Some specimens of *L. neritoides* are also found in rock pools, and Lebour considers that they migrate down to the pools before the eggs are shed into the water. *L. neritoides* is typical, however, in having fewer eggs per capsule than *L. littorea*. Its veliger larva is also

larger than that of *L. littorea* at metamorphosis. The eggs and egg capsules of *B. melanostoma* are larger than those of *B. auratum*, and their egg masses contain fewer eggs. The large egg capsules of *B. melanostoma* provide sufficient food for the embryos to develop into the shell stage before leaving the capsule. On the other hand, by the time the embryos of *B. auratum* develop to the veliger stage, most of the contents of the hyaline envelope have been used, and it is probable that under natural conditions they become free-swimming veliger larvae.

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EXPLANATION OF PLATES 1–5

PLATE 1

Fig. 1.—Section of male *Bembicium auratum*, showing the vas deferens (centre left) in the body wall anterior to the prostate; ×55; 10 μ; Mallory's triple stain.

Fig. 2.—Egg masses of *B. melanostoma*. ×1·7.

Fig. 3.—Egg masses of *B. auratum*. ×1·7.

PLATE 2

Fig. 1.—Neotype of *Bembicium melanostoma*, viewed from above, from the side, and from below. ×1·45.

Fig. 2.—*Bembicium* specimens viewed from above, side and below. Natural size.
(*a*) *Risella aurata* Quoy & Gaimard, Van Diemen's Land (type figure).
(*b*) *Risella aurata* Quoy & Gaimard, Van Diemen's Land (type figure).
(*c*) *Risella lutea* Quoy & Gaimard, Australia.

PLATE 3

Bembicium species viewed from above

(*a*) *B. melanostoma* from Port Adelaide River, South Australia.
(*b*) *B. melanostoma* from Beard Bay, South Australia.
(*c*) *B. melanostoma* from Robe, South Australia.
(*d*) *B. nanum* from Caloundra, Queensland.
(*e*) *B. nanum* from Devonport, Tasmania.
(*f*) *B. nanum* from Corny Point Beach, South Australia.
(*g*) *B. auratum* from Port Noarlunga, South Australia.
(*h*) *B. auratum* from Patawalonga Creek, South Australia.

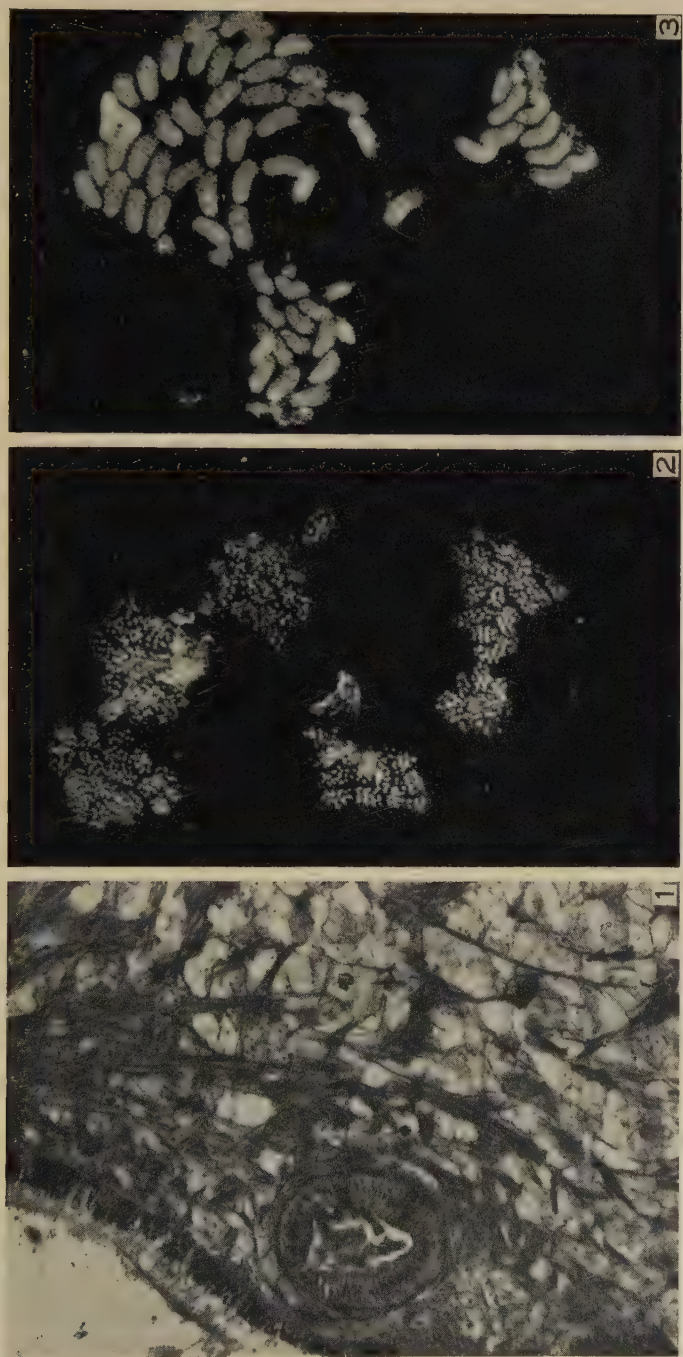
PLATE 4

Bembicium species viewed from the side. Lettering of specimens as in Plate 3

PLATE 5

Bembicium species viewed from below. Lettering of specimens as in Plate 3

THE GENUS BEMBICIUM



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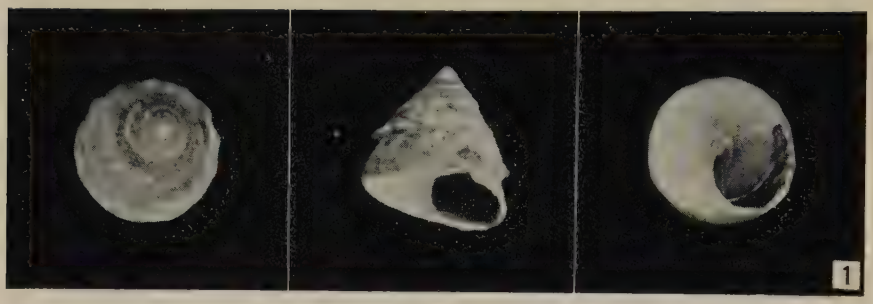

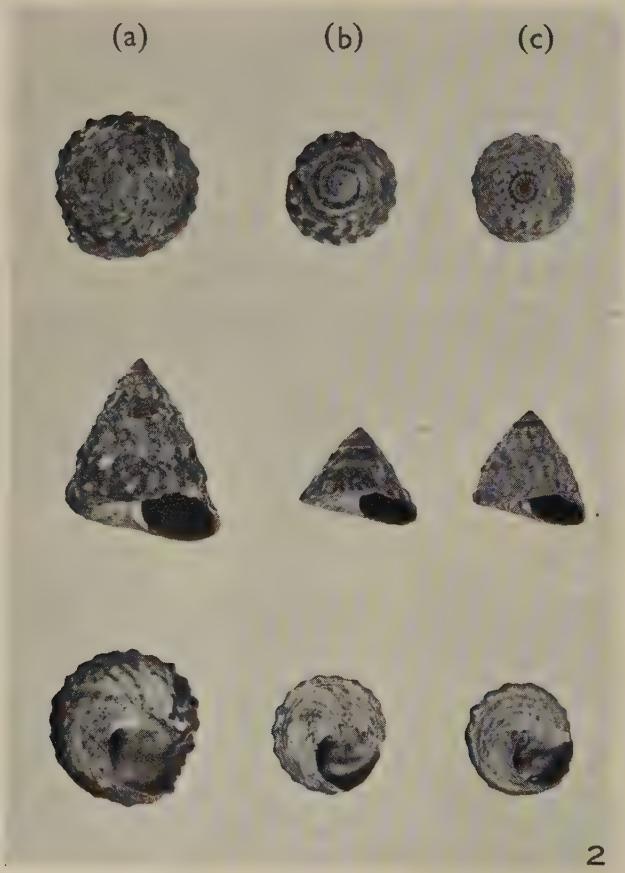

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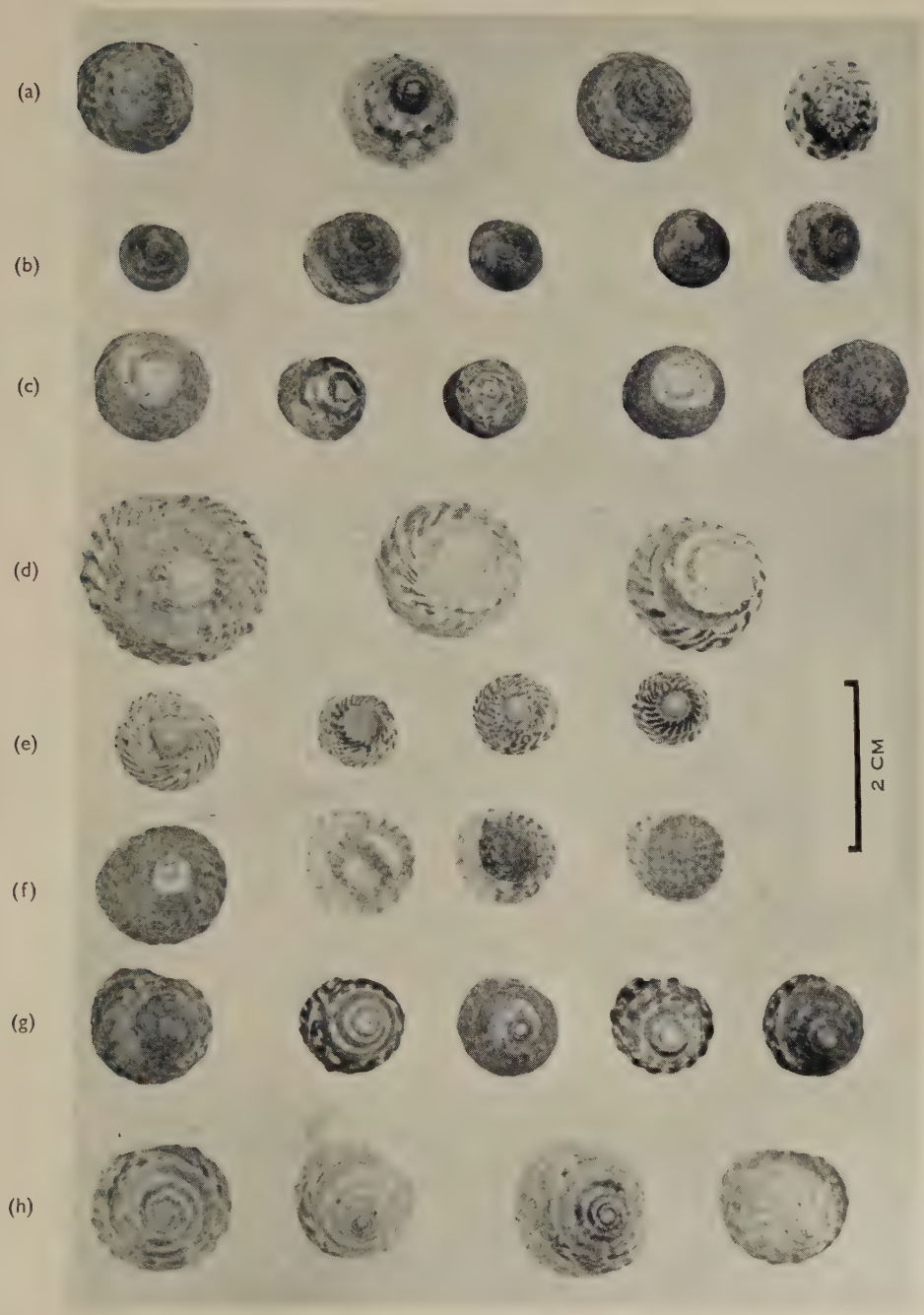

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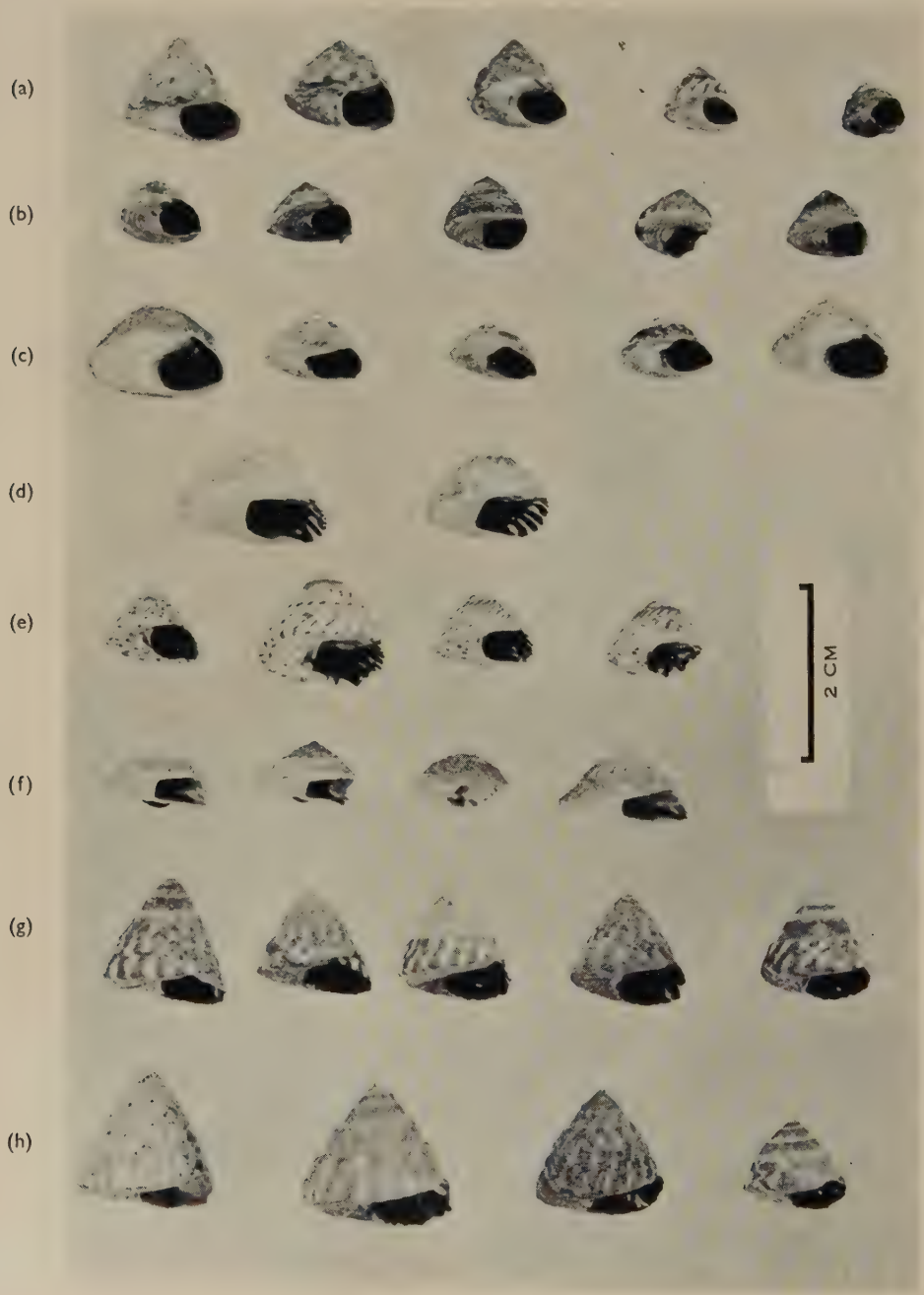

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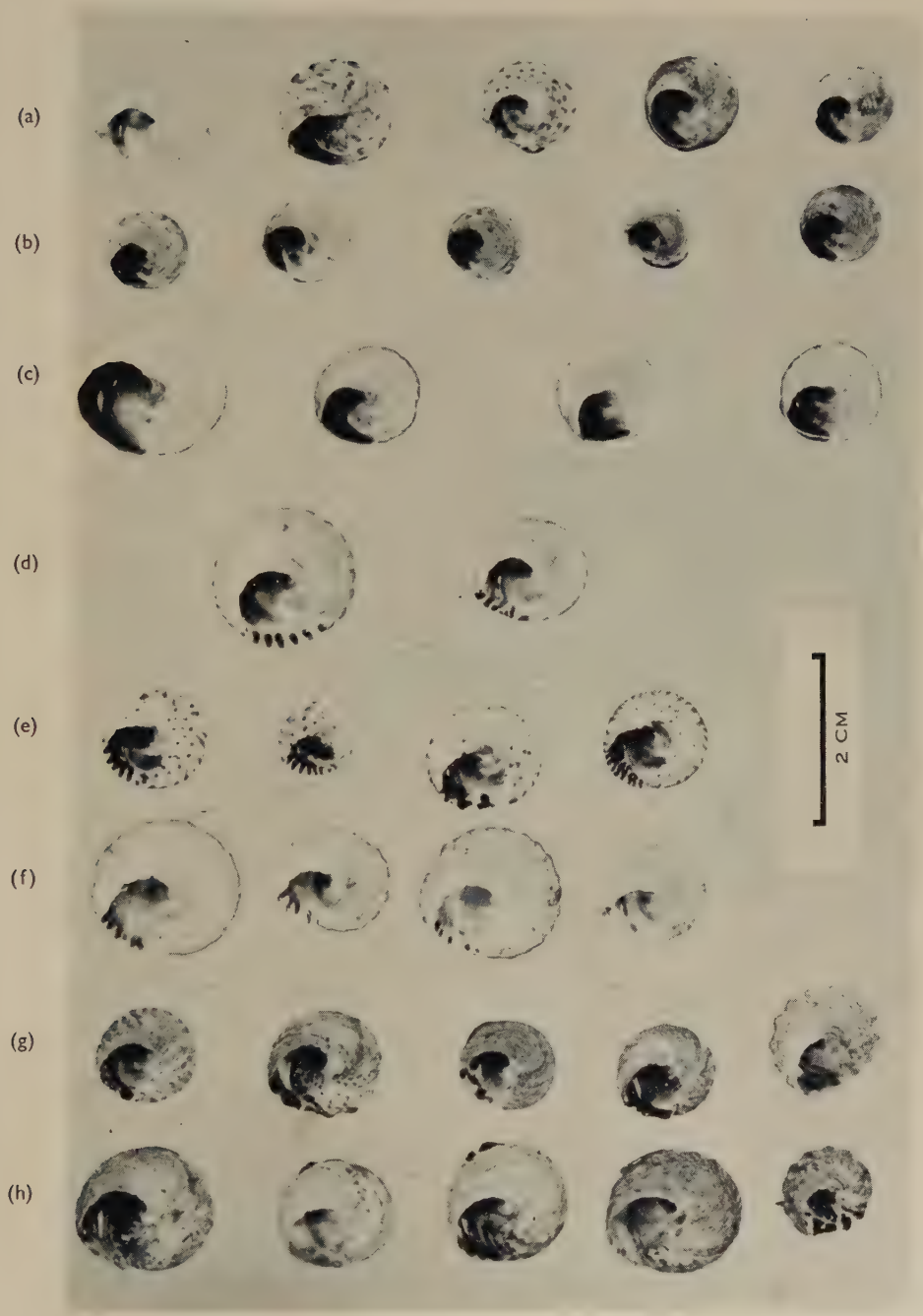

THE FAMILY TRIPHORIDAE (MOLLUSCA) FROM NORTHERN AUSTRALIA; ALSO TRIPHORIDAE FROM CHRISTMAS ISLAND (INDIAN OCEAN)

By C. F. Laseron*

[*Manuscript received April* 4, 1958]

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Summary

This is the first comprehensive study of the family Triphoridae (Mollusca) from northern Australia, which comprises the Solanderian and Dampierian zoogeographical provinces and, if the Queensland east coast be accepted as a separate province, the Banksian also. In all 101 species, divided into 17 genera, are figured and described, of which 91 species and 11 genera are proposed as new. In a separate section 14 species, divided into 10 genera, from Christmas Island in the Indian Ocean are described and figured, all the species and two genera being proposed as new. The Introduction includes a review of the literature and previous work, details of the proposed classification, and a key to existing genera.

I. Introduction

Outside of New Caledonia and the temperate regions of Australia the family Triphoridae has been largely neglected by conchologists throughout the world. There are several reasons for this. The shells are small, inconspicuous, not particularly attractive to the eye, they are not easy to detect, and, except in perfect condition, are very difficult to classify. Then, the family is a large one and there are a vast number of species, which can be identified only by careful microscopic examination. During the nineteenth century, when large collections from all over the world found their way to Europe, few evidently contained any specimens of the family, and the interest incited by the many large and striking novelties stifled interest in anything which would not grace a cabinet. The literature is therefore comparatively small, which for the present author is perhaps fortunate, as he is saved much time in endeavouring to untangle the mass of involved nomenclature and synonymy which confuses so many of the more popular families.

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The main distribution of living Triphoridae is probably in the Indian and Western Pacific Oceans, and a vast number of species exist, of which but a fraction has as yet been described and named. Work that has been done is mainly from widely separated localities, and at first sight suggests that the distribution is uneven, in the form of pockets of species concentrated in limited areas. But it is almost certain that intensive collecting in any part of East Africa, the Indian Ocean, the East Indies, the Philippines, or any continental or oceanic island in the Pacific would reveal an equal number of species, many of them endemic. The total may well ultimately run into four figures.

The first separation of any of the family as a distinct genus was by Blainville (1828) who described *Triphora gemmatum*, one of the species with the so-called "three apertures", from l'Isle-de-France, i.e. Mauritius. Deshayes about the same time (his work was published in 1831, but the relevant part bears 1824 on its title page) described a somewhat similar fossil shell, also with the "three apertures", as *Triforis plicatus* from the Eocene of the Paris Basin. The same author (1832) changed the spelling to *Triphoris*, but with the same type species, a course incompatible with accepted nomenclature, and which caused much confusion in naming by subsequent authors. No question of priority need however arise between *Triphora* and *Triforis*, as both can be considered good genera with distinctive characters.

Hinds (1843, 1844) described 20 species of the family, which he divided into three subgenera *Ino*, *Sychar*, and *Mastonia*. Of these ten were from the Strait of Malacca, seven from New Guinea or New Ireland, and the locality given for three was simply the Pacific Ocean. Hinds's work was very poor, the illustrations were too small to reveal essential characters, and the descriptions were short and wholly inadequate. Hinds's species cannot, however, be ignored, and efforts are here made to correlate those from New Guinea and New Ireland with Australian species, but this is done with no confidence, and until the types in the British Museum are properly illustrated and described, there will always be uncertainty.

Following Hinds, the work of what Hedley called the "London school" was even worse. A. Adams and Reeve described about 16 species, mainly from the China Seas or unknown localities, and of these the descriptions were on a par with those of Hinds, but no figures at all were provided. Of necessity these are entirely ignored. As Hedley (1899, p. 400) feelingly states: "Great numbers of the species of Adams, Hinds, Smith and others are inadequately represented in literature, and cannot be recognized without an inspection of the type in London. Either therefore no conchological work should be published except by residents of London, which is an absurd proposition, or these species must be ignored by naturalists."

The first mention of any species now known to occur in Australian waters was by Quoy and Gaimard (1834) who described *Cerithium* (now *Iniforis*) *violaceum* from New Ireland. In the Pacific, Triphoridae are particularly abundant in New Caledonia, where there are probably over 100 species, most of them still undescribed. From here Jousseaume (1884) described 18 species which he divided into six genera, using *Ino* and *Mastonia* of Hinds, and adding *Iniforis*, *Mastoniaeforis*, *Euthymia*, and *Viriola*. *Ino* and *Euthymia* have since been found to be preoccupied and have been replaced by *Inella* Bayle (1879) and *Euthymella* Thiele (1929). Hervier (1897, 1898)

described a further 29 species from Lifu in the nearby Loyalty Islands, using the same generic designations as Jousseaume. Of these species many are probably endemic, but some undoubtedly range as far as the Great Barrier Reef in Queensland.

From Australian tropical waters Watson (1886) described two species from the Torres Straits, in addition to one from Fiji and three from the Atlantic. Melvill and Standen (1899) described one species and recorded one of Hinds's species, also from the Torres Straits. Again in the Pacific Hedley (1899) recorded nine species from Funafuti Atoll in the Ellice Group, four of which he proposed as new. His other determinations were mostly tentative, and most will need new specific names. Hedley (1909) later described one species from the Hope Islands, Queensland, which unfortunately is now synonymized under one of Watson's species. At the time he contemplated a full review of the Queensland species, but stated privately that he was appalled at the multitude of species and the difficulties of the task for which he could not spare the time. That concludes all the work done to date on tropical forms from Australia and the adjacent seas.

More attention has been paid to the family in the Australian temperate provinces. Apart from individual species described by several authors at various times, the New South Wales species were reviewed by Hedley (1902) and later by Laseron (1954). May (1923) figured all the known species from Tasmania (the Bassian Province), and Cotton and Godfrey (1931) dealt with those from southern Australia (the Flindersian Province). None of the species from the temperate south occur in the tropical provinces, except where there is some slight overlap at the junction of the two areas.

The Solanderian and Dampierian Provinces.—It is too early to determine just what part the Triphoridae play in the general ecology and in the delimitation of what have been termed the Solanderian and Dampierian zoogeographical provinces. When Hedley (1904, p. 880) proposed these names he defined their boundaries as from Torres Straits to Moreton Bay for the Solanderian, and from Torres Straits westwards to the Abrolhos Islands for the Dampierian. Whitley (1932, p. 166) later proposed that Solanderian should be restricted to the Great Barrier Reef, and that Banksian be used for the fauna of the east Queensland coast. The present author, in recent papers on the small molluscs of northern Australia, has followed Hedley in taking the boundary of the two provinces as Torres Straits, but recent work by Endean (1957) on the Echinodermata throws doubt on this delimitation. He suggests that while Solanderian should be restricted to the Great Barrier Reef, the Dampierian should be extended through the Torres Straits to include the shore of the Queensland mainland.

How far the Mollusca will bear out this hypothesis it is as yet impossible to say. The student of the Mollusca is still primarily concerned with the problems of taxonomy, and the immediate necessity is to classify the vast number of species in the whole area. Only when this is done can intensive and quantitative collecting determine the limits of distribution and ecological association. For this reason no discrimination is made in this paper between the Solanderian and Dampierian Provinces, but the general designation "northern Australia" is used to cover the seas

from the Cambridge Gulf in the north-west to Moreton Bay in Queensland and to a limited extent the southern shore of New Guinea.

One curious feature in the distribution of the Triphoridae is nevertheless here noted. That is the concentration in the vicinity of Moreton Bay and on the extreme north coast of New South Wales of a number of species which seem endemic to this area and are found neither north nor south. The actual area from Caloundra to the extreme north coast of New South Wales is by general consent included in the Peronian Province; yet at Caloundra only one true Peronian species of Triphoridae was recognized, *Aclophora maculosa* (Hedley). The common species at Caloundra are *Nanaphora caloundra*, sp. nov.; *Coriophora nigrogranosa*, sp. nov.; *Aclophora robusta*, sp. nov.; *Nanaphora tricolor*, sp. nov.; *Aclophora grandiosa* (Laseron); and *A. conferta*, sp. nov. Of these, the first two have been found only at Caloundra, *A. robusta* was found further north at Port Curtis, and the last three occur also on the north coast of New South Wales. In addition *Euthymella pannata* was found at Angowrie, in New South Wales, but at the last minute a live specimen was obtained at Heron Island, and was selected as the holotype. Though found within the Peronian Province, none of these species is Peronian, and this is asserted confidently, as the present author has done much intensive collecting of Triphoridae in New South Wales, and has examined nearly all the material collected by others. They apparently constitute a small localized fauna of their own.

Sources of Material.—The material which forms the basis of this paper is, as far as is known, practically all that has ever been collected from northern Australia, with the exception of the few species in the British Museum obtained by the Challenger Expedition and by Melvill and Standen. None of the large collections from the Great Barrier Reef which have been sent abroad seems to have contained any Triphoridae, or if so they have not been mentioned in any of the numerous papers published. Australian collectors also, with a few exceptions, have generally overlooked them. Among Australian institutions the Australian Museum, Sydney, alone has accumulated a collection of northern species, mainly through the efforts of such keen collectors as Hedley, Brazier, McCulloch, and Kesteven. The late Charles Hedley, particularly, over many years assiduously sorted out and put by every specimen he could obtain, and this material has proved invaluable in this research. In later years the present author's son, John Laseron, has made large collections, mainly from Darwin, Bowen, Port Curtis, the Capricorns, and Hervey Bay. M. Ward has made dredgings off Darwin, T. Iredale has sorted out many species from Michaelmas Cay, Lindeman Island and Low Isles, and G. Whitley, by dredging in Cambridge Gulf in north-west Australia, obtained some sand which contained two undescribed species. From Christmas Island in the Indian Ocean T. Iredale has also made available a unique little collection from which no less than 14 undescribed species of Triphoridae were sorted out. These have been described in a separate section at the end of the main paper. A small additional amount of material was obtained from several sources from such present-day collectors as Garrard, Mrs. Kerslake, and Miss Thornley. Finally, from outside the state, F. S. Colliver of the Brisbane University sent for examination the few specimens in the Shirley Collection.

TABLE 1

GEOGRAPHICAL POSITION OF LOCALITIES

Locality	Lat. (S.)	Long. (E.)
North-west Australia		
Cambridge Gulf	15° 0′	128°10′
Darwin	12°20′	130°50′
Gulf of Carpentaria		
Mapoon	12° 0′	141°45′
Mornington Island	16°30′	139°30′
Torres Straits and New Guinea		
Thursday Island	10°59′	142°12′
Albany Passage	10°39′	142°35′
Warrior Island	9°50′	142°58′
Darnley Island	9°35′	143°45′
Murray Island	9°54′	144° 0′
Port Moresby	9°25′	147° 8′
Queensland East Coast		
Cairns	16°54′	145°44′
Bowen	20° 1′	148°16′
Whitehaven Bay	20°16′	148°53′
Yeppoon (Keppel Bay)	23°25′	150°15′
Gladstone and Port Curtis	23°58′	151°20′
Bustard Head	24° 0′	152°15′
Hervey Bay	25° 0′	153° 0′
Caloundra	26°49′	153° 9′
Moreton Bay	27° 0′	153°15′
Great Barrier Reef		
Two Isles	15° 0′	145°30′
Hope Islands	15°45′	145°30′
Endeavour Reef	15°50′	145°40′
Low Isles	16°23′	145°35′
Michaelmas Cay	16°35′	146° 0′
Fitzroy Island	16°55′	146° 1′
Eclipse Island	18°46′	146°37′
Lindeman Island	20°30′	149° 4′
Brampton Island	20°47′	149°18′
Wreck Reef	22°10′	155°28′
Capricorn Group*	23°30′	152° 0′
Lady Elliott Island	24° 7′	152°46′
North Coast, New South Wales		
Angowrie	29°26′	153°20′
Indian Ocean		
Christmas Island	10° 0′	105°42′

*Heron Island and Masthead Island.

This apparently is all the material available for study. It is undoubtedly far from complete, as there are considerable geographical gaps and areas from which no collecting has been done at all, but to hold up publication at this stage would probably mean its indefinite postponement. Sufficient material is available to give at least a general picture of the constitution and distribution, previously entirely unknown, of the family over this area, and also to provide a foundation on which future work can be based.

To summarize the results, 101 species are now figured and described from northern Australia, 91 of which are proposed as new. In addition several species have been figured but left unnamed, pending the acquisition of better material. The 101 species have been divided into 17 genera, 11 of which are proposed as new. From Christmas Island in the Indian Ocean 14 species with two additional genera are all proposed as new. These evidently belong to a different zoogeographical province.

Table 1 shows the geographical position of all localities from which material was obtained for research.

II. Classification

From shell characters alone, which are all that is available, the classification of the Triphoridae presents the same difficulties that beset so many other molluscan families. Members of the family itself are easy to recognize, mainly by the elongated spire, the aperture, and almost invariably the sinistral coiling of the shell.* But within the family the characters are so uniform that, if only a few species existed, one or perhaps two genera would be sufficient to cover them. Such a simple classification is, however, complicated by the great number of species. Probably more than a thousand species live in the Pacific and Indian Oceans, and subdivision into genera is necessary, if only to facilitate the running down and identification of specific forms. Whether the various groups into which the family is now divided be termed genera, subgenera, or merely sections is immaterial. The view is here expressed, as it has been in previous papers, that the use of subgenera, unless based on sound, phylogenetic grounds, can be very misleading, as it assumes a relationship that may in no sense exist. If generic names alone are used, it serves to identify groups, and future discussion of their more intimate relationships is still open.

The main difficulty in the Triphoridae is that there are few outstanding characters by which groups of species can be readily separated and recognized. The aperture alone enables a broad division into three groups, "simple", "twofold", and "threefold", but even here there are many borderline species, and in others the degree of maturity can obscure the differences between types. Other characters cannot be used singly but only in combination. Those used for generic separation are chiefly form, sculpture, and the protoconch.

Opinions differ about the use of keys in molluscan identification, but with the Triphoridae some form of key becomes absolutely necessary. The value of a key lies in its practicability. The key here provided was worked out early in the preparation of this paper, and as more and more species came to light it was in continual

*The latter character is not quite invariable, as at least one undescribed species from the Miocene of Balcombe Bay, Victoria, with a typical aperture of the "threefold" kind, is dextral in its coiling.

use, needing only slight modifications as the end approached. It has in this way stood up to a practical test.

Of the genera here used six had been proposed by earlier authors either as full genera or subgenera, and 13 are now proposed as new. This brings the total number of genera, including those not yet identified from northern Australia, to 24. Of the 101 species figured and described most seem endemic to limited areas, but three have been identified with New Caledonian species, and several others range to New Britain and the islands to the north. No doubt future collecting will show others to range through the arc of islands bordering the east side of the Coral Sea, but most of the species inhabiting the oceanic islands of the Pacific will probably be found to be endemic, having developed in long isolation.

III. Shell Characters

The Aperture.—One of the most characteristic features of the family is the aperture and its varying development after maturity. By maturity is meant that stage when the shell has attained its full size, the animal is no longer growing, the body whorl is completed, and it is assumed that while the animal has still much of its life to lead it is fully adult. At this stage there is a great similarity in the aperture of all species. There is a short columella column which is grooved on its inner margin by the anterior canal. The posterior canal is a shallow sinus or at the most a narrow slit. The anterior margin of the aperture is thin and bent in a sharp fold developing into a spur, which may fall short of or reach the columella column and thus partially enclose the anterior canal. This type of aperture is here called "simple", and a great many species do not progress further. It is noteworthy that all the species from the temperate Australian provinces have simple apertures.

The next stage of development takes place after maturity is reached, and consists in the continual growth of the margins of the aperture into a short, round tube, which is thin and externally nearly smooth, showing little trace of the sculpture on the spire. The posterior canal remains open as a deep sinus or slit, or it may be a circular orifice connected to the outer margin of the aperture by a narrow slit. The anterior canal is, however, completely enclosed, so that it opens quite within the aperture, while externally it may be prolonged into a comparatively long tube. This type is the so-called "two apertures" of some writers. A great many tropical species have this type of aperture including *Mastonia*, *Viriola*, and other genera. Unless a series of specimens of the one species is available for study difficulty is sometimes experienced, as specimens which have just attained maturity still retain the simple type of aperture, and their true affinities are not revealed.

In the third or ultimate type, the so-called "three apertures", the true aperture may be extended into a circular tube of considerable length, the anterior canal is also tubular, and the posterior canal is quite enclosed and becomes tubular to a greater or lesser extent. The appearance is very striking: three tubes, sometimes of nearly equal size, project from the base of the spire, only one of which is the true aperture.

If the threefold aperture is taken as the final stage of evolution it was reached very early in the history of the family, for it is found in the earliest fossils known. The family probably originated in the Cretaceous, for by the early Tertiary it had a

world-wide distribution. Triphoridae are fairly abundant in the European Tertiary from the Eocene onwards, and *Triforis* with a typical threefold aperture was found in the Eocene near Paris. In Australia specimens are very common in the strata at Balcombe Bay in Victoria, which are generally placed as Miocene. Here there are at least 15 or 16 species, and though many of the apertures are broken, sufficient are intact to prove that all three types of apertures occur.

The Protoconch.—As with other families of small gasteropods the protoconch has proved of the utmost value in specific determination, but when used for generic differentiation it must be considered as but one of other characters which may be of equal or even greater importance. Amongst the great number of recent species the protoconchs fall into two main groups, or possibly three. These occur indiscriminately associated with other characters, and cannot be used alone for major divisions. Of the two main types of protoconch the commonest is multi-whorled, conical, and often acuminate, the whorls bearing either a sharp single or double spiral keel crossed by numerous fine axial threads or cords. There is seldom a terminating varix, and adult sculpture may begin either abruptly or gradually. The next most common type is short and few-whorled, the apex sometimes mammillate, the nucleus broad and dome-shaped, sometimes tilted, incipient sculpture beginning on the first or second whorl. In the third type, characteristic of the genus *Isotriphora* Cotton, the nucleus is entirely submerged in the summit, the initial whorls are planoid and fully sculptured, and the whole apex is domed. The smooth, glassy, subulate protoconch, so common in the Cerithiopsidae, was not detected in any of the species examined.

Examination of a number of specimens of Miocene Triphoridae from Balcombe Bay showed a much greater diversity of protoconchs, most of them very different from those of recent species. They are beautifully preserved and clearly show every detail. Without any attempt at specific determination, as most if not all the species are undescribed, six of the fossil protoconchs are here figured for comparison. Of these Figure 250 is of the type so common in living species and Figure 252 is very close to that of the tropical *Inella gigas* (Hinds) (cf. Fig. 26). Another interesting protoconch is that shown in Figure 243. This is very close to that of the living *Isotriphora* Cotton, having the same immersed nucleus and early, fully sculptured, planoid whorls. As the aperture and sculpture of the mature shell are also of the same type, this might well be of the ancestral stock from which *Isotriphora* was derived. Nothing approaching the protoconchs shown in Figures 247, 248, or 251 has, however, been observed in any living species. Just what significance the protoconch has in the phylogenesis of the Triphoridae it is as yet impossible to say, and long and intensive research will be necessary before the question can even be partly answered.

Sculpture.—The sculpture of the Triphoridae is of primary importance, both specifically and generically. The interaction of spiral and axial sculpture was probably developed over a considerable geological period, resulting in the varying types seen in living species. Amongst the fossil species are many in which spiral sculpture is predominant, consisting of a number of fine spiral keels, sometimes four or five, with the spaces between nearly smooth, or crossed by obscure, oblique, axial ribs (Fig. 353). The whorls may be flat (Fig. 253) or rounded (Fig. 255). Such predominant spiral sculpture can be seen in some living genera, with fine axial threads between as in

Viriola Jousseaume, smooth between as in *Teretriphora* Finlay, or with the keels in two orders as in *Solosinister* Laseron. Most of the species of these groups are uncommon and confined to deeper water, and are possibly survivors of earlier types. In some fossil species axial sculpture is strong, consisting of oblique ribs which are broken into ill-defined gemmules (Fig. 254). Sculpture of this type has not been noted in living species.

The development of rounded gemmules seems to have come later. The gemmules are evidently the culmination of axial sculpture where it overrides the spiral keels, passing through the stages where the gemmules are connected both spirally and axially by narrow ribs to where the gemmules are isolated, perfectly rounded, and large. If this be the course evolution has followed, *Mastonia* Hinds, a large tropical group, is of comparatively recent origin. In most genera the earliest whorls have only two rows of gemmules, and in *Mastonia* there are only two rows throughout, but in *Mesophora* and *Coriophora* a third small row develops about half-way down the spire. In other genera such as *Notosinister* and *Aclophora* there are three rows from the earliest mature whorls, and in *Tetraphora* there are four persistent rows. Extra rows of gemmules and smooth spiral keels are invariably present on the base of the body whorl.

Loose or tight coiling of the spire is considered of considerable importance, and there is a marked difference between such genera as *Notosinister*, *Tetraphora*, and *Aclophora* which have the sutures deeply channelled, and *Mastonia* in which the sutures are barely discernible.

A distinct type of sculpture is found in the genera *Inella* and *Euthymella*. In both of these the gemmules are few in number, spirally elongated, overridden by sharp, spiral keels, and connected axially by broad, rounded columns.

Form and Size.—The Triphoridae as a whole can be considered to have small shells, but there is considerable difference in their relative size. For purposes of description those which have a length of less than 5 mm are termed small, those between 5 mm and 10 mm are called medium, and those over 10 mm large.

The form and number of whorls vary considerably. All the species are more or less elongate in the axis of the spire, but some are exceedingly attenuate with almost no taper and may then possess upwards of 25 whorls, as in *Inella gigas*. At the other extreme are the short, inflated species, with highly convex spires and restricted at the base, such as *Nanaphora* and *Opimaphora*. In between are the great majority of species, all more or less conical in form, but sometimes with the lower portion of the spire nearly cylindrical. The sides of the spire may be straight or slightly convex, this character giving a distinct facies, but these differences are only specific.

In some species there is considerable variation in both size and form. For instance in a long series of *Mastonia ruber* from the Capricorn Group the variation was so great that it was at first thought that more than one species was indicated, but every gradation between the extremes of size and inflation occurred and all other characters were identical. Many other species are, however, remarkably constant in both form and size, and these characters then become a good guide in specific determination.

Colour.—The colour is on the whole remarkably constant in each species, and in such a difficult family, is extremely useful in the recognition of species. Some allowance must be made for possible fading after death, but where a definite colour pattern exists it generally persists, and can often be recognized on greatly worn and broken specimens. A peculiar colouring found on some species as in some of the Cerithiopsidae is a uniform reddish purple which fades after exposure sometimes to a pale violet. It is thought that this colour may be due to specialized food, possibly a sponge or coral, and that occasional lack of this particular food causes variation in the one species to a pale brown, though nearly always there is a tinge of the characteristic purple. This is seen in *Coriophora marceda.*

IV. Key to Genera of Recent Triphoridae

1.	Posterior canal tubular (so-called threefold)	2
	Posterior canal a notch or sinus (so-called simple or twofold)	6
2(1).	With 2 rows of gemmules	3
	With 3 rows of gemmules	5
3(2).	Rows of gemmules unequal, shell acicular	*Contraforis*, gen. nov.
	Rows of gemmules equal, shell conical	4
4(3).	Protoconch multi-whorled, acuminate	*Inforis* Jousseaume
	Protoconch few-whorled, blunt	*Epiforis*, gen. nov.
5(2).	Sutures channelled	*Triphora* Blainville
	Sutures not defined	*Mastoniaeforis* Jousseaume
6(1).	Sculpture wholly or in part smooth, spiral keels	7
	Sculpture of rows of raised gemmules	10
7(6).	Sculpture of spiral keels and rows of gemmules	*Orbitophora*, gen. nov.
	Sculpture of smooth spiral keels only	8
8(6).	Protoconch mammillate	*Sychar* Hinds
	Protoconch acuminate, several whorls	9
9(8).	2 or 3 spiral keels, axial threads between	*Viriola* Jousseaume
	3 smooth, broad, spiral keels, no axial threads	*Teretriphora* Finlay
	2 sharp smooth spiral keels, with small keel between	*Solosinister* Laseron
10(6).	Gemmules spirally elongated	11
	Gemmules rounded	13
11(10).	Several rows of gemmules of different orders, not connected by axial columns	*Torresophora*, gen. nov.
	Gemmule rows connected by broad axial columns	12
12(11).	Shell exceedingly attenuate	*Inella* Bayle
	Shell short and stout	*Euthymella* Thiele
13(10).	Protoconch acuminate of 4 or more whorls	14
	Protoconch broad, of under 4 whorls	20
14(13).	Shell attenuate	15
	Shell elongate but not attenuate	16
	Shell inflated, restricted at the base	19
15(14).	Attenuate, whorls from 10 to 16	*Subulophora*, gen. nov.
	Acicular, whorls over 20	*Liniphora*, gen. nov.
16(14).	Sutures not defined	17
	Sutures channelled	18
17(16).	2 close rows of gemmules, a small median row in later whorls	*Mesophora*, gen. nov.
	2 distant rows of gemmules, connected by strong axial chords	*Magnosinister* Laseron
18(16).	3 equal rows of gemmules	*Notosinister* Finlay
	4 equal rows of gemmules	*Tetraphora*, gen. nov.

19(14). Shells over 5 mm, whorls more than 10, 2 rows of gemmules .....*Mastonia* Hinds
Shells under 5 mm, mature whorls less than 10, very inflated ..*Opimaphora*, gen. nov.
20(13). Protoconch completely immersed in summit .....*Isotriphora* Cotton
Protoconch not completely immersed in summit 21
21(20). Shells under 5 mm, very inflated, and restricted at the base ....*Nanaphora*, gen. nov.
Shells generally over 5 mm, not inflated 22
22(21). 3 rows of gemmules, sutures channelled 23
2 rows of gemmules, a small median row on later whorls .....*Coriophora*, gen. nov.
23(22). Gemmules rounded, rows equal .....*Aclophora*, gen. nov.
Gemmules irregular, middle row largest .....*Distophora*, gen. nov.

Note on Key.—The genera *Sinistroseila* Oliver (1914, p. 523) and *Cautor* Finlay (1927, p. 384) are not included in the above key, as insufficient information is available to decide their exact positions. The type species of *Sinistroseila* is *Triforis incisus* Pease, is unfigured, and comes from the Sandwich Islands. The generic characters given by Oliver are: "shell turretted, sinistral, sculptured with spiral ridges only". It thus comes very close to *Viriola* of which it may be a synonym. The type species of *Cautor* is a New Zealand deepwater species *Triphora lutea* Suter, and it is stated that it has two heavy spiral keels and a blunt protoconch. The nearest genus to this is *Sychar* Hinds, but only actual comparison of the shells can determine their relationship or differences.

V. Description of Northern Australian Species

All types, paratypes, specimens illustrated and material examined, if not already in the Australian Museum, Sydney, are now presented to that institution. They have been uniformly arranged and labelled in special containers, and comprise what is probably a unique collection in a form readily available for future reference.

Genus INIFORIS Jousseaume

Iniforis Jousseaume, 1884, p. 235.

Type species *Iniforis malvaceus* Jousseaume.

Jousseaume divided the recent species with the so-called three apertures into two series, *Iniforis* for those with two rows of gemmules and more than 15 whorls, and *Mastoniaeforis* for those with three rows of gemmules and 15 whorls or less. He ignored the original *Triphora* Blainville (1828, p. 344), the type of which, *Triphora gemmatum*, came from l'Isle-de-France (Mauritius). This has three rows of gemmules and from the original descriptions and figures *Mastoniaeforis* may well be a synonym, except that it shows no distinct sutures between the whorls while *Triphora* shows a channelled suture. There is no information available about the protoconchs, but from the illustrations *I. malvaceus* has an acuminate apex, and it is assumed that the protoconch is multiwhorled with spiral keels, and that this is characteristic of the genus *Iniforis*. Fortunately the question of the synonymy of *Mastoniaeforis* under *Triphora* does not arise in this paper, as none of the Australian species yet examined has three rows of gemmules.

Iniforis violaceus (Quoy & Gaimard)

Figs. 1–5

Cerithium violaceum Quoy & Gaimard, 1834, p. 134, pl. 55, figs. 22, 23.

Much confusion has arisen about the identity of *violaceus*, and the name has been indiscriminately applied to several species, particularly *ruber* Hinds, which

are either purple or violet in colour. Hedley (1899, p. 442) rightly points out, however, that the only criterion is the original figure, and this shows distinctly that the posterior canal is produced as a short tube, and that the species is an *Iniforis* and not a *Mastonia* of which *ruber* is the type species.

Specific points to be noted are the colour, the protoconch, and sculpture. The colour when fresh is purple, rather duller than in *Mastonia ruber*, fading in beach specimens to a dull violet. The protoconch is conical, has 6 whorls, crossed by 2 spiral keels very close together, and these are crossed by fine axial threads. The gemmules are in 2 rows; they are large and rounded, 18 to the whorl, connected spirally by narrow ridges, and the sutures are shallow but distinguishable. The aperture can be misleading, as it is only in very mature specimens that the posterior tube is developed. In a series from Low Isles collected by Iredale all stages were noticed, from the twofold aperture as in *Mastonia* to the fully developed threefold type.

The type locality is New Ireland, and the species has a wide range, at least from New Guinea down the full length of the Great Barrier Reef. Figures 1–3 are of a specimen from Eclipse Island collected by Hedley (C.7268 in Australian Museum) and its length is 6·5 mm. Figures 4–5 are from a specimen from Port Moresby with an exceptionally long protoconch, though otherwise identical.

Specimens in the Australian Museum from Lifu labelled *Mastonia ducosensis* Jousseaume are again really an *Iniforis* and are very close to *violaceus*, except that they have an even longer and more attenuate protoconch.

Iniforis violaceus evanidus, subsp. nov.

Figs. 6–8

Specimens from a number of localities on the Barrier Reef were at first thought to be a distinct species, until careful comparison showed they had no essential difference from *I. violaceus* except in colour. Instead of the uniform dull purple or violet they are all of a pale cream or lilac, against which the deep chocolate of the protoconch stands out in striking contrast. The specimen selected as holotype and four paratypes are from Michaelmas Cay (T. Iredale), the type being 5·6 mm in length. There is considerable variation in size and width, and specimens from Murray Island (C. Hedley) and Barrier Reef off Cairns (D. Pitt) are smaller than the type. On the other hand a series collected alive by J. Laseron under coral blocks on Heron Island range from mature specimens smaller than the type to comparative giants over 10 mm in length.

The aperture, like the typical *violaceus*, comes just within the stage of development characteristic of *Iniforis*, and that only in odd specimens of considerable maturity. In most specimens the posterior canal has not yet become tubular, but is a circular orifice still connected by a narrow slit with the outer margin of the main aperture, thus resembling *Mastonia* as in the type (Fig. 8).

Though this subspecies cannot be considered a geographical race, it has been thought appropriate to give it a distinctive name as a convenience to future research.

Iniforis spp.

Figs. 9 and 10

Two single specimens of what appear to be separate species of *Iniforis* are here figured for future reference, though neither is considered perfect enough for accurate specific description. Figure 9 is from the Barrier Reef off Cairns (D. Pitt), C.46014 in the Australian Museum, and is 5 mm in length. It is white, with 2 rows of very large, rounded gemmules, the upper row slightly smaller than the lower, 13–14 to the whorl. It is very like *Iniforis jousseaumei* Hervier from Lifu, and may possibly be that species, but better material is needed before this can be decided.

Figure 10 came from 17–20 fm, Masthead Island (C. Hedley), C.21017 in Australian Museum, and is 3·8 mm in length. It is a shorter, broader species than Figure 9, has a different contour, is yellowish in colour, and the gemmules are smaller and more numerous. The only known species with which it can be compared is *Iniforis cornuta* Hervier from Lifu.

Iniforis zonata, sp. nov.

Figs. 11 and 12

Shell large, conical, attenuate, white and vitreous, with a narrow band of bright orange-brown crossing the lower row of gemmules on about three-fourths of the spire. Protoconch unknown, the apical whorls missing on the type. Remaining whorls about 24, the sutures barely distinguishable. Sculpture of 2 spiral keels, above which rise large, rather irregular gemmules, the upper row the larger, 12 to the whorl, the body whorl with an extra partially tuberculate keel on the base, which is hardly restricted. True aperture round, tubular but not greatly extended, the posterior canal a short, circular tube, well behind the margin of the aperture, the anterior canal tubular, opening within the aperture, elongated, straight, almost in the line of the spire, crossed at the base by 3 folds. Length 10·2 mm.

Locality.—Warrior Island, Torres Strait (C. Hedley), C.5808 in Australian Museum, holotype.

Remarks.—Though this species was described from a single specimen without a protoconch there should be no difficulty in its future recognition. It is by far the most attenuate of the species of *Iniforis*, and the colour pattern and aperture are distinctive.

Iniforis porrecta, sp. nov.

Fig. 13

Shell of medium size, slender, regularly conical, colour white. Protoconch unknown. Type imperfect, 9 whorls remaining, sutures distinct but not deep. Sculpture of 2 rows of rounded gemmules, 13 to the whorl, the lower row very large and close together, the upper row small, neither spiral nor axial connections apparent. Aperture of the threefold type, the true aperture tubular and long, the anterior canal a conical tube with several transverse folds and produced in the axis of the spire, the posterior canal tubular and slightly shorter, swollen near the base and restricted at its aperture. Length 5·3 mm.

Localities.—Murray Island (C. Hedley), holotype; Low Isles (T. Iredale).

Remarks.—Though this species was established on specimens without their apices, there should be no difficulty in its future recognition. The form is slender but less so than in *I. zonata*, but the most distinctive character is the great disparity in size between the two rows of gemmules. In this it approaches the genus *Contraforis* proposed later in this paper for a Christmas Island species, but *Contraforis* is extremely attenuate with long whorls and the rows of gemmules wide apart, giving it a distinct facies.

Genus EPIFORIS, gen. nov.

Type species *Epiforis australis*, sp. nov.

Aperture of the threefold type, the sculpture and form like *Iniforis*, but the protoconch short, broad, and cylindrical without apparent axial threads. This genus is separated on the protoconch alone, following the classification adopted in other cases, as for instance between *Opimaphora* and *Nanaphora*, and *Notosinister* and *Aclophora*. Apart from the type, two further species from Christmas Island are described later in this paper.

Epiforis australis, sp. nov.

Fig. 14

Shell small, bottle-shaped, broad at the base, slender towards the summit, with a convex spire, slightly restricted at the base; colour upper part white, lower part of spire pale straw with touches of brown between the gemmules. Protoconch a dome-shaped nucleus right on the summit, followed immediately by 2 whorls with 2 spiral keels, the uppermost the larger, which gradually break into gemmules. Total whorls about 10, the sutures not defined. Sculpture of 2 rows of gemmules, the upper much the larger, the gemmules large, about half their diameter apart, 14 to the whorl, rising from sharp well-defined spiral keels which override the gemmules in narrow, sharp ridges. The body whorl has an extra row of gemmules on the base. Aperture of well-developed threefold type, the main aperture tubular and prolonged, the posterior canal well developed as a rapidly tapering conical tube, the anterior canal long and tubular, tapering, with a broad fold near its base, straight, and extended in the line of the spire. Length 4·7 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype.

Remarks.—Apart from the form and protoconch, the most distinctive character is the way the spiral keels override the large gemmules.

Genus ORBITOPHORA, gen. nov.

Type species *Orbitophora iredalei*, sp. nov.

Medium-sized shells of distinctive sculpture, with 2 smooth, spiral keels, between which is a row of small round gemmules. The protoconch in the type species is cylindrical, short, with a single spiral keel overridden by strong axial cords. Aperture of the twofold type, the posterior canal a notch or slit, the anterior canal tubular.

Orbitophora iredalei, sp. nov.

Figs. 15 and 16

Shell of medium size, solid, conical, the sides of the spire nearly straight, colour cream with a band of red-brown covering the central row of small gemmules. Protoconch in type missing, but an immature paratype shows it to be short and cylindrical with a large tilted nucleus, followed by 2 whorls with a single spiral keel overridden by strong axial cords. Mature whorls 13, sutures distinct. Sculpture of 2 equal, smooth, sharp spiral keels, between which is a smaller keel, broken into numerous small, rounded gemmules, about 30 to the whorl, connected to the keels above and below by fine axial threads. An extra anterior smooth keel is on the body whorl which has a flat base bearing still another thin smooth keel. Aperture subquadrangular, subtubular, extended anteriorly, the margins slightly reflected, the anterior canal entirely enclosed and opening within the aperture, the posterior canal a deep, rounded sinus. Columella column nearly straight, rounded anteriorly. Length 10 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype and two paratypes.

Remarks.—The colour, sculpture, and form should make the future recognition of this species easy.

Orbitophora albomarmorata (Hervier)

Figs. 17–19

Viriola trilirata Deshayes var. *albomarmorata* Hervier, 1897, p. 263.

Deshayes's species is from Mauritius, and Hervier proposed the varietal name for specimens from Lifu characterized by brown colouring irregularly blotched with white. No figure was given and the description was confined to two lines, but specimens from Michaelmas Cay and the Capricorns were identified by comparison with a series in the Australian Museum labelled according to Hervier, from Lifu, the type locality. No differences could be detected, and the slight variation in form and sculpture occurs in all localities. That there may be no doubt in future identification a fuller description is now added.

Shell of medium size, conical, rather stout with convex sides, colour red-brown with irregular white patches, generally on the lower spiral keel. Protoconch conical, shaped like a beehive, of 5 whorls, acuminate, the nucleus small, the other whorls short, each with a double spiral keel, overridden by axial cords. Mature whorls from 12 to about 15, sutures no deeper than the furrows between the keels. Sculpture of 3 spiral keels, the lowermost the largest, the medium keel smallest, the upper and lower keels restricted at intervals, about 12 to each whorl, the median keel broken into short lengths which appear as partially rounded gemmules, with no axial connecting ridges. This character, which takes the species into *Orbitophora*, is not always apparent, as the median keel sometimes appears smooth mainly due to wear. The aperture is of the twofold type, the main aperture becoming tubular after maturity; the anterior canal is tubular, broad, and oblique, the posterior canal a deep U-shaped sinus right on the suture.

Figures 17 and 18 are of a specimen 6 mm long, one of a series collected by T. Iredale from Michaelmas Cay; it is rather smaller than the average. Figure 19 is

from the Capricorn Group (J. Laseron), taken alive under stones, and it has the small median row of gemmules particularly distinct. A specimen from Low Isles is doubtfully referred here as it is nearly white, but it may be faded.

Genus VIRIOLA Jousseaumè

Viriola Jousseaume, 1884, p. 238.

Type species *Viriola bayani* Jousseaume.

The type species came from New Caledonia, and the generic characters are so distinctive that some Australian species are confidently assigned to it. The shell is very elongate and acuminate, the aperture is twofold, the posterior canal a deep slit but not tubular, the main aperture shortly tubular, the columella pillar deeply grooved for the anterior canal which is oblique and often greatly extended. The sculpture is of 2 or 3 smooth, spiral keels, which are axially finely striate between. The protoconch is multiwhorled, acuminate, with spiral keels overridden by axial threads.

Very close to *Viriola* is *Sychar* which was proposed as a subgenus by Hinds (1843, 1844) for a new species *vitreus* from the Straits of Malacca. This from Hinds's limited description has sculpture very similar to *Viriola*, but the whorls are rounded and the summit mammillate. No species of this type have yet been found in Australia.

Viriola excelsior (Melvill & Standen)

Fig. 20

Triforis (*Ino*) *excelsior* Melvill & Standen, 1899, p. 166, pl. 10, fig. 5.

The type locality is Torres Strait which makes the identification reasonably sure, though the brief description does not quite fit the figure given, and the authors state that there is no interstitial pitting between the keels. This statement may possibly be discounted, however, as the authors in other cases have been very careless about such details, and Melvill, who did the actual description, is reputed to have dispensed with any aids to magnification.

The specimen here figured is from 6 fm, Cairns Reef (C. Hedley), and is 22·5 mm long. In colour it is nearly white, but is possibly somewhat faded. Other specimens are from Murray Island, C.29472 in Australian Museum. The sculpture is very close to *V. corrugatus* Hinds, but the shell is even more slender and has many more whorls. The anterior canal is also greatly extended, oblique, and tubular. The posterior canal is similar. The protoconch is unknown.

Viriola corrugata (Hinds)

Fig. 21

Triphoris (*Ino*) *corrugatus* Hinds, 1843, p. 18; 1844, pl. 8, fig. 12.

As with all Hinds's species, unless the type in the British Museum can be examined, there is no certainty of identification, but the name has been generally accepted for a species with a wide range in the Pacific. The type locality is New Guinea, and Hedley (1899, p. 448) records it from Funafuti, and discusses its further

range to various localities, including Lifu, New Caledonia, and Queensland. A specimen from 5–10 fm, Hope Islands (C. Hedley), C.27294 in Australian Museum, light yellow in colour, can be taken as typical, and shows no difference when compared with specimens from New Caledonia. Specimens identical in all structural details are common on the coast of the Queensland mainland, and a long series was collected by J. Laseron living under stones at Bowen. These differ, however, in colour, and are deep red-brown and almost black. A similar specimen from Brampton Island (J. Laseron) is here figured, its length 17 mm. Features of the species, apart from the sculpture, are the long attenuate shell, the large, oblique, tubular anterior canal, and the tubular extension of the main aperture. The posterior canal is a deep slit.

Genus TORRESOPHORA, gen. nov.

Type species *Torresophora elongata*, sp. nov.

Form of shell like *Viriola*, large, long, and attenuate, sculpture like *Euthymella*, of several spiral keels of 2 or 3 orders, broken into spirally elongated gemmules, but without axial connecting columns. The protoconch is multiwhorled and attenuate, the aperture twofold, the true aperture tubular after maturity, the anterior canal tubular and opening within the aperture, the posterior canal a notch or slit.

Torresophora elongata, sp. nov.

Figs. 22 and 23

Shell large, conical, very elongate and acuminate, colour a uniform cream white. Protoconch slender, of 4 whorls, slightly worn in the type, but the third and fourth whorls faintly keeled. Mature whorls approximately 20 but sutures hardly distinguishable. Sculpture of several spiral keels of 3 orders, broken into gemmules, 12–13 to the whorl, the gemmules spirally elongated with sharp summits, but not connected axially by columns, the grooves between nearly smooth. The spiral keels are in 3 orders, alternately small, medium, small, large, the large one apparently at the bottom of the whorl. The earlier whorls have the gemmules more rounded; in the later whorls they are flatter. The body whorl has an extra row of gemmules anteriorly; the base is nearly flat, and bears a single thin, smooth keel. Aperture nearly circular, becoming tubular, expanded anteriorly, entirely enclosing the anterior canal, which is tubular, oblique, and well extended. Posterior canal a narrow notch. Length 14 mm.

Locality.—Darnley Island, Torres Strait (C. Hedley), C.7525 in Australian Museum, holotype; Masthead Reef (C. Hedley).

Remarks.—There is no other species with which this species can be compared. In form it is like a *Viriola*, the sculpture is close to *Euthymella* and also *Inella gigas* but without the axial connecting columns. The specimen from Masthead Reef conforms in all characters, except that the gemmules in the later whorls are rather more rounded than in the type. Though it has been difficult to find good material for description it is apparently not a rare species, as fragments have been seen from a number of localities.

Genus INELLA Bayle, 1844

Ino Hinds, 1843, p. 18. (Non *Ino* Samsuelle 1817.)
Inella Bayle, 1879, p. 27, nom. nov. for *Ino* Hinds (preocc.).

Type species *Triphoris* (*Ino*) *gigas* Hinds.

Hinds used the misspelt *Triphoris* Deshayes as a genus dividing it into three subgenera *Ino*, *Sychar*, and *Mastonia*. His 1844 paper is practically a reprint of that published in 1843, except that figures were added. In both papers descriptions are hopelessly inadequate, both of the subgenera and species, being confined to a couple of lines of Latin and omitting most of the essential characters. Fortunately the illustrations give a clue, but they are too small to show details of the apertures, sculpture, and apices. Hinds's description simply states that the shell is cylindrical, elongate, and acuminate, and from the description and figure of the type species it is gathered that it is 11 lines long, with 25–28 whorls and 4 rows of gemmules which are punctate between. Other species placed by Hinds in *Ino* are a mixture of types and do not assist in its determination. The type locality is New Guinea; Melvill and Standen (1899, p. 166) recorded *Triforis gigas* from Mer in the Torres Strait, and now specimens from Darwin are tentatively identified as that species.

From the Darwin specimens the description of *Inella* is now amplified to include relatively large shells which are extremely narrow and acuminate, with from 20–30 whorls. The aperture is simple, the posterior canal a notch or short slit, the columella column short and straight. Sculpture is of 3 or 4 rows of gemmules, more or less spirally elongate, and joined from row to row by narrow axial ribs.

Use of the protoconch may need further generic revision in the future. A second species here described has a normal multiwhorled protoconch (Fig. 29), but a very young specimen also from Darwin, tentatively identified as *I. gigas*, shows an extraordinary protoconch (Fig. 26), which is almost identical with that of an undescribed Miocene fossil from Balcombe Bay in Victoria (Fig. 252). This is so unlike the protoconch of any other known living species that it suggests some hereditary connection with a remote past.

Inella gigas (Hinds)

Figs. 24–26

Triphoris (*Ino*) *gigas* Hinds, 1843, p. 18; 1844, pl. 8, fig. 1.

The specimen which is here figured, and which generally fits Hinds's meagre description and figure, was collected by M. Ward from 15–20 fm off Point Charles, Darwin. It is not quite perfect, is 25 mm long, 4 mm wide, is extremely attenuate and has approximately 23 whorls remaining. The colour is pale straw, the aperture is simple, the posterior canal is a shallow slit, but the specimen may not be quite mature. The sculpture is, however, distinctive, though it does not quite fit Hinds's description. There are 4 rows of gemmules, one very narrow and marking the sutures, the gemmules number 16 to the whorl; they are spirally elongated and connected, and connected row to row by rather broad axial columns. The protoconch (Fig. 26), apparently from the same species, came from a very young specimen

from the same locality. The species evidently is confined to deeper water as it has not so far been seen from shore collections.

Inella acicula, sp. nov.

Figs. 27–29

Shell relatively large, conical, extremely slender, colour cream or pale straw. Protoconch slender, of 4½ whorls, with a small tilted nucleus, sculpture beginning as a single spiral keel, a double keel on the last 2 whorls, axial striations faint. Mature whorls approximately 26, sutures hardly distinguishable. Sculpture of 3 rows of gemmules on the later whorls, 2 only on the early whorls, 16 gemmules to the whorl, the median row the smallest, the gemmules spirally elongated and connected, flattened posteriorly, not rounded but rising into blunt points, connected row to row by axial columns, a fourth row of gemmules on the body whorl. Aperture simple, subquadrate, the outer margin thin and slightly expanded, posterior canal triangular, the anterior spur not reaching the columella. The anterior canal is shallow, the columella column bent, crossed by obscure folds and ridged vertically adjacent to the aperture. Length 15·5 mm, width 2 mm.

Localities.—Darnley Island (C. Hedley), C.7526 in Australian Museum, holotype; also C.8080 from the Torres Strait; 5–8 fm Murray Island, C.29998; Michaelmas Cay (T. Iredale); 5–10 fm Hope Islands (C. Hedley); 20 fm Lindeman Island (T. Iredale); 4–14 fm Albany Passage (C. Hedley).

Remarks.—Apart from the protoconch which eventually may separate it generically from *I. gigas*, this species is smaller and in relation to its length even more attenuate. It also differs in details of sculpture, having three instead of four rows of gemmules. It is a fairly common species, constant in its characters, but specimens are generally broken, and it is difficult to get perfect material. Specimens from the Hope Islands are smaller and even more acicular than the type, but otherwise conform in all characters.

Genus EUTHYMELLA Thiele

Euthymia Jousseaume 1884, p. 237. (Non *Euthymia* Stel 1876.)
Euthymella Thiele 1929, Vol. 1, p. 219, nom. nov. for *Euthymia* Jousseaume (preocc.).

Type species *Euthymia regalis* Jousseaume.

This is a distinctive genus, the type species of which came from New Caledonia. It is a medium-sized to large shell, broad and heavy, the aperture of the twofold type, the mature whorls numbering about 15. The sculpture resembles *Inella*, but is much more exaggerated. There are from 4 to 5 rows of gemmules on each whorl; the gemmules are in the form of lozenges, elongated spirally, and may be arranged in series, alternately large and small, with one row generally much larger than the others. The gemmules are connected axially by strong ribs which give a columnar appearance to the sculpture. The protoconch is not known in the type species, but in others it is short and mammillate.

Euthymella regalis (Jousseaume)

Fig. 30

Euthymia regalis Jousseaume, 1884, p. 265, pl. 4, fig. 18.

The type locality is New Caledonia. The specimen illustrated is from Wreck Reef (C. Hedley), C.32381 in Australian Museum, and is 10 mm long without the apical whorls. It matches specimens from New Caledonia very well except that it is a little broader, and there are minor differences in the aperture which may be due to the stage of maturity. Another slenderer specimen is from Low Isles (T. Iredale), and two specimens from Murray Island (C. Hedley), C.29469, also appear to be this species, though both are imperfect.

Euthymella pannata, sp. nov.

Fig. 31

Shell of medium size, lower portion of spire nearly cylindrical, the last 3 whorls nearly equal, upper portion conical, colour white, with numerous, small, irregular patches of chocolate, base brown. Protoconch in type imperfect, only 2 whorls remaining, but evidently cylindrical and obtuse, the remaining whorls with faint spiral keels. Mature whorls 10, sutures not discernible, but their positions probably marked by a narrow spiral keel which is broken into numerous elongated gemmules. The other sculpture is of 3 rows of gemmules, the lowest much the largest, the other 2 equal, gemmules large and spirally elongated, 12–13 to the whorl, rising above defined spiral keels, and connected axially by broad columns. Body whorl has 2 extra rows of gemmules on flattened base. Aperture round, expanded, and subtubular, anterior spur reaching the columella, anterior canal quite enclosed, posterior canal a V-shaped sinus. Columella column rather long, oblique, tapering anteriorly. Length 7 mm.

Localities.—Heron Island, under coral blocks (Miss B. Dew), holotype; Angowrie, near Clarence River, New South Wales (A. A. Cameron).

Remarks.—This species was first seen from Angowrie, and the type was first chosen from that locality, though it was anticipated that this would be a tropical species. A good specimen found alive at Heron Island confirmed this, and is now selected as the holotype. The species is closest to *E. regalis* (Jousseaume), but differs mainly in the colour pattern and by the extra broken keel marking the sutures.

Euthymella alternata, sp. nov.

Fig. 32

Shell of medium size, conical with slightly convex sides, moderately stout, the main row of gemmules white, the remainder ochreous. Protoconch too worn for accurate description, but short, not more than 2 or 3 whorls, sculpture apparently beginning on the second whorl. Mature whorls about 13, the sutures not discernible. Sculpture of 4 rows of gemmules, 14 to the whorl, in 3 series, alternating large, small, medium, small, large, throughout the spire, but judging from the body whorl, the large row is apparently at the bottom of each whorl. Two extra rows of gemmules on the base of the body whorl. Gemmules elongated spirally, joined by a narrow spiral

keel, which overrides them, forming a sharp ridge on their summits. The axial ribs joining the gemmules are broad, low, and not conspicuous. Aperture rounded, approaching the twofold type, not quite tubular, but expanded anteriorly to enclose the anterior canal, which is short, opens within the aperture, and is externally tubular, anteriorly rounded, and slightly oblique; posterior canal an ill-defined notch. Length 6·5 mm.

Locality.—Murray Island, C.29470 in Australian Museum, holotype and one paratype.

Remarks.—Compared with *E. regalis* this species is much smaller, the gemmules are more numerous, the axial ribs are less defined, and the anterior canal is tubular, shorter, and less oblique. From *E. tribialis* (Jousseaume) from New Caledonia it differs in details of the aperture and sculpture, and *tribialis* has a slender, many-whorled protoconch. A good recognition point is provided by the alternating bands of white and ochre.

Euthymella pilea, sp. nov.

Figs. 33 and 34

Shell small, conical, with nearly straight sides, apex blunt, colour white with one or two touches of yellow. Protoconch relatively large, a tilted nucleus followed by a large inflated whorl which bears an indistinct spiral keel and another barely discernible; no axial sculpture detected. Mature whorls 11, sutures indistinguishable. Sculpture of 3 rows of gemmules, one large and two small, the large row apparently at the bottom of the whorl. The gemmules are 12 to the row and, as in other species, spirally elongated, joined to each other by a narrow keel which overrides them, and connected axially by broad columns which are, however, low and not well defined. An extra row of gemmules is on the base of the body whorl which is slightly excavate, with another slight, smooth keel just above the columella. Aperture relatively large, semi-tubular, greatly expanded, and shovel-like anteriorly; quite enclosing the anterior canal which has its opening within the aperture, is large, straight, and rounded anteriorly; posterior canal an ill-defined triangular notch. Length 4·5 mm.

Locality.—Barrier Reef off Cairns (D. Pitt), C.46023 in Australian Museum, holotype and two paratypes.

Remarks.—This species is smaller than the preceding, it has straighter sides and a broader base, the sculpture differs in its details, also the aperture, and the broad, slightly mammillate protoconch is also distinctive.

Genus MASTONIA Hinds

Mastonia Hinds, 1843, p. 18.

Type species designated by Jousseaume *Triphoris* (*Mastonia*) *ruber* Hinds.

Hinds's meagre description of his subgenus states simply that it is acuminate and medially tumid, and he includes a number of species of varying characters, some of which have little relationship. The type designated by Jousseaume (1884, p. 236) fortunately has very definite characters which are common to a number of other species here assigned to it. The protoconch is slender, of several whorls, either singly or

doubly keeled, the keels crossed by axial cords. The form is bottle-shaped, slender at the summit, medially tumid, and restricted at the base. The sculpture consists of 2 rows of smooth, rounded gemmules, separate from each other, often large, without spiral or axial connections, and the sutures are indistinguishable. The aperture varies with the individual but develops to the twofold type, the true aperture becoming tubular, the anterior canal opening within the aperture, and the posterior canal progressing from a shallow sinus to a circular perforation which, however, never becomes tubular as in *Iniforis*.

Mastonia ruber Hinds

Figs. 35 and 36

Triphoris (*Mastonia*) *ruber* Hinds, 1843, p. 19; 1844, p. 30, pl. 8, fig. 15.
Triphora ruber (Hinds), Hedley, 1899, p. 441. fig. 29.

The type locality is New Britain, but Hedley published the first adequate description and figure from specimens from Funafuti, pointing out that it is probably the commonest and most widely distributed species in the western Pacific, ranging from the Great Barrier Reef to New Caledonia and to the oceanic islands beyond. Specimens here examined are from a long series living under coral blocks at Heron Island (J. Laseron) and another long series from Murray Island (C. Hedley), C.29467 in Australian Museum. The specimen illustrated is from Heron Island, its length 8·4 mm. From all localities it is seen to be very variable in size and relative width, but the bright purple colour is distinctive, and details of the sculpture, aperture, and protoconch are constant.

Mastonia iris, sp. nov.

Figs. 37–39

Shell of medium size, bottle-shaped, the apex acuminate, the lower portion of spire tumid, restricted at the base, protoconch yellow to pale brown, upper row of gemmules pure white, lower row yellow, the 3 basal keels pale orange. Protoconch slender, conical, of 5 whorls, nucleus small, next whorl nearly smooth, remainder with a single spiral keel and faint axial threads. Mature whorls 10, sutures only distinguishable by alternating colour bands. Sculpture of 2 equal rows of large rounded gemmules, close together, 16 to the whorl, without apparent spiral or axial connections, the body whorl with the upper row of gemmules large, below which is a smaller row, with 2 additional partially tuberculate spiral keels on the rounded base. Aperture twofold, the true aperture tubular, round, expanded anteriorly enclosing the anterior canal which opens within the aperture, is tubular, wide, slightly oblique, rounded anteriorly, and crossed by a rounded fold; posterior canal a semicircular orifice connected by a narrow slit with the outer margin. Length 5 mm.

Locality.—Barrier Reef off Cairns (D. Pitt), C.46025 in Australian Museum, holotype and three paratypes.

Remarks.—In form and sculpture there is practically no difference between this species and *M. ruber*, but fortunately the colour pattern enables the two species to be readily separated. The critical specific character is, however, the protoconch, that of *ruber* having a double keel, while *iris* has but a single one.

Mastonia sp.

Figs. 40 and 41

Two specimens from Port Moresby collected by C. Hedley, C.8528 in Australian Museum, are identical in all essential characters with *M. ruber* Hinds, except that they are smaller than the smallest seen of that species and have quite a different colour pattern. The gemmules are also slightly smaller. In colour the protoconch is pale brown; this is followed by 2 pure white whorls; then 3 whorls are a pale purple. The remaining whorls have the upper row of gemmules a pale lilac and the lower row bright yellow. The columella is pale yellow. The length of the specimen illustrated is 4·7 mm. The colour is nearer to *iris* than *ruber* but the protoconch has a double keel like *ruber*. More material is needed to decide if they are specifically or racially separable from *ruber*, but in the meantime the figure and brief description should be useful for future reference.

Mastonia queenslandica, sp. nov.

Figs. 42, 43, 46, and 47

Shell small to medium, conical with convex sides, slightly restricted at the base, colour a uniform bright cream. Protoconch conical, acuminate, of 6 whorls, with a single sharp spiral keel crossed by axial threads. Mature whorls 10, sutures not defined. Sculpture of 2 rows of even, smoothly rounded gemmules, of moderate size, 16 to the whorl, about half their diameters apart, without spiral or axial connections. Two extra rows of smaller gemmules appear anteriorly on the body whorl. with a smooth spiral keel on the base. Aperture rounded, expanded, on extremely mature specimens only becoming twofold, the true aperture then becoming subtubular and enclosing the anterior canal, which is broad, slightly oblique, recurved at its extremity, and rounded; posterior canal a deep, rounded sinus. Length 4·6 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype (Figs. 42 and 43); Lindeman Island (T. Iredale) (Figs. 46 and 47); under stones Darnley Island (J. Brazier); Eclipse Island (C. Hedley), C.7274 in Australian Museum; Capricorn Group (J. Laseron); Barrier Reef off Cairns (D. Pitt), C.46026; Low Isles (T. Iredale); Bowen (J. Laseron).

Remarks.—This is a common and widely distributed species on the Barrier Reef, and it also ranges to the Queensland coast. It is remarkably constant and the uniform bright cream colour is a good recognition point. The only variation is in size, and the Lindeman Island specimen (Fig. 46) is 8 mm in length. *M. queenslandica* has at different times been referred to *M. aegle* Jousseaume (a New Caledonian species) but in the absence of authentic specimens it has been impossible to verify this. Hedley (1899, p. 439, fig. 27) gave a full description of a Funafuti shell which he identified as *aegle*, and this certainly differs from *queenslandica*, having fewer and larger gemmules, which are not rounded but truncate posteriorly and more or less facetted. Nearer in appearance to *queenslandica* is *Mesophora pallenta*, sp. nov., but this has a different colour, and the appearance of a third row of gemmules on the lower half of the spire takes it into a different group (see Figs. 44 and 66).

Mastonia obtusa, sp. nov.

Figs. 48 and 49

Shell of medium size, bottle-shaped, apex acuminate, lower portion of spire inflated, restricted at the base. Colour of protoconch brown, the next 2 whorls pale, remainder with alternating rows of pale and dark red-brown, the lower portion of body whorl and base chocolate. Protoconch acicular, of 5 whorls, each with a sharp single keel which is overridden by coarse axial threads. Remaining whorls 11, sutures not defined. Sculpture of 2 rows of small rounded gemmules, close together, 20–22 to the whorl, the deeper coloured row slightly larger than the other and on the body whorl becoming axially elongated with a tendency to break into two. Below this on the body whorl are 2 additional rows of irregular, almost square gemmules, and below again 2 smooth spiral keels on the base. Aperture relatively small, rounded, extended, and subtubular, enclosing the anterior canal which opens within the aperture; posterior canal a deep, narrow slit right on the suture, widening but not circular within. Columella column very short and broad, rounded anteriorly. Length 6·5 mm.

Locality.—Capricorn Group (J. Laseron), holotype.

Remarks.—In form this resembles both *ruber* and *iris*, differing from *ruber* in colour, sculpture, and by the single-keeled protoconch, and from *iris* by a slight difference in colour pattern, but chiefly by the more numerous, closer, and smaller gemmules, and by the very obtuse columella column.

Mastonia funebris Jousseaume

Figs. 50 and 51

Mastonia funebris Jousseaume, 1884, p. 262, pl. 4., fig. 15.

The species has been identified by comparison with specimens in the Australian Museum so labelled from the type locality, New Caledonia. It is a common and widely spread species on the Barrier Reef, the specimen figured being from the Barrier Reef off Cairns (D. Pitt), C.46008 in Australian Museum. It is 4·7 mm in length. Other specimens studied are from Masthead Island (C. Hedley), C.19041; and 20 fm off Endeavour Reef (A. McCulloch). Specimens from Masthead Island are rather larger than that figured, the gemmules are slightly closer together and more numerous, but all other characters correspond.

Recognition is easy by the colour pattern, spiral bands of from orange to red-brown covering the lower row of gemmules, the upper row being white. Nearly the same colour pattern occurs in *Mesophora sardonyx*, sp. nov., but in that species the upper row of gemmules and the sutures are chocolate. The protoconch is long, slender, and acuminate, of 6 whorls, with a single spiral keel crossed by axial threads. The aperture barely reaches the twofold stage, and in specimens of normal maturity is simple, the anterior spur reaching the columella, the posterior canal a deep V-shaped sinus.

Genus MESOPHORA, gen. nov.

Type species *Mesophora bowenensis*, sp. nov.

Mesophora is very close to *Mastonia*, and is separated largely on account of the great number of species involved. It has a similar protoconch, elongate, with

from 5–7 whorls, which may be singly or doubly keeled, overridden by axial threads. The shells are, however, generally more elongate and less tumid medially, and the sculpture, though on the early whorls of 2 rows of gemmules only, has a third median row developing about half-way down the spire, and the gemmules are generally connected by ridges both spirally and axially. The aperture also is not quite as far developed as *Mastonia*, and the true aperture though extended does not become tubular. The anterior spur reaches the columella and may completely enclose the anterior canal, but the posterior canal is quite open, and at its greatest development a deep U-shaped sinus.

Mesophora bowenensis, sp. nov.

Figs. 52–55

Shell large, conical, elongate, acuminate, spire only very slightly convex, colour a deep uniform brown, almost black. Protoconch relatively small, conical, acuminate, of 5 whorls, the last 3 with a single spiral keel crossed by fine axial threads. Mature whorls 13, sutures discernible but not well defined. Sculpture of 2 main rows of relatively small gemmules, rounded, 18 to the whorl, about their own diameter apart, rising above well-defined, narrow spiral keels. Between the main rows and about half-way down the spire a narrow thread develops, which gradually breaks into narrow, elongated gemmules. An extra row of small gemmules is on the base of the body whorl, and anterior to this 2 smaller, smooth, rounded keels. Aperture rounded, laterally and anteriorly expanded, but not tubular, the anterior spur crossing the columella and covering but not enclosing the anterior canal, posterior canal a deep, narrow sinus, right on the suture. Columella column short, slightly oblique, rounded anteriorly. Length 10 mm.

Localities.—Bowen, alive under rocks (J. Laseron), common, holotype (Figs. 52, 53) and 11 paratypes selected; Fitzroy Island (J. Brazier), C.8726 in Australian Museum; Hervey Bay (J. Laseron); Cleveland, Moreton Bay, in mud (Mrs. J. Kerslake); Port Curtis (J. Laseron) (Figs. 54, 55).

Remarks.—The species is rather variable in size, and some mature specimens are smaller and others still larger than the type. In none is the aperture more developed than in the type. The deep, almost black colour, and small shining gemmules are good recognition points. The species has not been seen on the Barrier Reef. but it is common on and seems typical of the southern half of the Queensland coast. A curious feature of the Port Curtis specimens is that there is a slight difference in the protoconch, though the specimens cannot otherwise be told apart. The protoconchs are in both cases very small, and it is difficult to detect details even under high magnification, but those from Port Curtis all lack the final keeled whorl. It would appear that from some unknown local condition the juvenile stage ended earlier than elsewhere, but it is considered that, though the protoconch is of critical importance in the delimitation of species, there is here no essential difference to warrant either specific or racial separation. A specimen from Port Curtis (Figs. 54, 55) is here figured for comparison.

Mesophora pavimenta, sp. nov.

Figs. 56 and 57

Shell small to medium in size, broadly conical, acuminate, spire with convex sides and restricted at the base, colour a uniform yellow-brown, the earlier whorls lighter in colour. Protoconch small and acuminate, of 4 whorls, at first nearly smooth, 2 spiral keels gradually developing which are overridden by very fine axial threads. Mature whorls 12, sutures barely discernible. Sculpture of 2 main rows of small, rather irregular gemmules, about 24 to the whorl, closely packed together and rising above well-defined spiral keels, appearing nearly square and flattened in the later whorls. About half-way down the spire a third median row of very small gemmules appears, and on the body whorl there are 4 rows, the uppermost the largest, while on the rounded base is another nearly smooth spiral keel. Aperture rounded, expanded laterally and anteriorly but not tubular, anterior spur reaching the columella and covering anterior canal; posterior canal a shallow V-shaped sinus. Columella column short, broad, oblique, and anteriorly truncate. Length 4·7 mm.

Localities.—Under stones, Darnley Island (J. Brazier), holotype; 5–8 fm Murray Island (C. Hedley); Port Moresby (C. Hedley), C.8518 in Australian Museum.

Remarks.—The numerous, closely packed, and nearly square gemmules distinguish this from other species of *Mesophora*, but in this and other characters it is so close to *Coriophora capricornia*, sp. nov., that in the absence of the protoconch, it is impossible to tell them apart. The latter species, however, has a short mammillate protoconch, and from that character alone has been placed in a different genus (see Fig. 121).

Mesophora torpedo, sp. nov.

Figs. 58 and 59

Shell of medium size, elongate, cylindrical, conical towards the summit, with an acuminate apex, restricted towards the base, protoconch brown, the remainder cream with irregular brown patches. Protoconch small, slender, and acuminate, of 5 whorls, the first dome-shaped, remainder with a single spiral keel crossed by very fine axial threads. Mature whorls 12, sutures barely discernible. Sculpture of 2 equal rows of gemmules on the first half of the spire, with a third small median row developing on the anterior half, the body whorl with 4 nearly equal rows, and 2 additional smooth spiral keels on the base. The gemmules are small and imperfectly rounded, 20 to the whorl, about half their diameter apart, and rise above well developed spiral keels. Aperture rounded, expanded but not tubular, the anterior spur reaching the columella, the posterior canal a small but deep rounded sinus. Columella column very short, very broad, oblique, and rounded anteriorly. Length 5·6 mm.

Localities.—5–8 fm Murray Island (C. Hedley), holotype and two paratypes; Michaelmas Cay (T. Iredale); dredged off Point Charles, Darwin (M. Ward).

Remarks.—The distinctive form, shaped almost exactly like a torpedo, and the colour should facilitate the future recognition of this species.

Mesophora purpurea, sp. nov.

Figs. 60 and 61

Shell large, elongate, conical, spire very slightly convex, only slightly restricted at the base, colour a uniform dull pale purple. Protoconch not quite complete, only 3 complete whorls and part of another remaining, but these bear a double spiral keel crossed by axial threads. Mature whorls 14, sutures barely discernible. Sculpture at first of 2 rows of well-defined, rounded gemmules, very close together, 20 to the whorl, rising above low but defined spiral keels, and connected row to row by broad axial ribs. Half-way down the spire a third median row of small gemmules gradually develops, and on the body whorl there are 4 nearly equal rows, with an additional smooth spiral keel on the base. Irregular ridges also cross the columella column. Aperture rounded and expanded, subtubular, the anterior spur crossing the columella and entirely enclosing the anterior canal, posterior canal a V-shaped sinus. Columella column short, broad, slightly oblique, truncate anteriorly. Length 9 mm.

Localities.—Masthead Island (C. Hedley), holotype; Heron Island (J. Laseron); Murray Island (C. Hedley).

Remarks.—This is a distinctive species standing out by its form and colour from other species of *Mesophora*. In appearance it actually most resembles *Iniforis violaceus*, but it can be readily separated from that species by the smaller, more numerous gemmules, and by the third median row developing half-way down the spire. The aperture is, however, the chief criterion. In the absence of a long series of specimens it is impossible to say if that of the type has attained its full development, but from the shape of the anal notch it is not likely that it would ever attain a three-fold nature. The specimen from Murray Island is smaller and relatively narrower than the type, but otherwise conforms in all characters.

Mesophora mellita, sp. nov.

Figs. 62 and 63

Shell of medium size, elongate, conical, apex acuminate, spire very slightly convex, texture subvitreous, protoconch brown, columella red-brown, upper row of gemmules white, remaining rows covered by thin, honey-coloured bands. Protoconch conical and acuminate, of 5 whorls, with a single spiral keel crossed by fine axial threads, adult sculpture beginning abruptly. Mature whorls 11, sutures defined and deep. Sculpture in earlier whorls 2 rows of even rounded gemmules rising above defined spiral keels. In the later whorls the gemmules in the upper row are round and well defined, close together, 18 to the whorl; then a small median row develops and this and the lower row have ill-defined gemmules which are stellate in appearance. Two additional smooth spiral keels are on the base of the body whorl. Aperture as in other members of the genus, circular, laterally and anteriorly expanded; the anterior spur a sharp fold which partially encloses the anterior canal; posterior canal a deep, narrow U-shaped sinus. Columella column nearly straight, not oblique, narrowed, and rounded anteriorly. Length 6·4 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and 10 paratypes.

Remarks.—This is a handsome species, readily recognizable by the colour and also the irregularity and stellate appearance of the lower row of gemmules.

Mesophora iniqua, sp. nov.

Figs. 64 and 65

Shell of medium size, elongated, conical, apex acuminate, spire very slightly convex, protoconch and columella brown, remainder a uniform deep cream. Protoconch small, acuminate, of 4 whorls, the last 3 with a double spiral keel crossed by fine axial threads. Mature whorls 12, separated by deep sutures. Sculpture in the early whorls 2 equal rows of gemmules, a third median row gradually developing, while the lowest row becomes much the larger. The gemmules are rounded, 16 to the whorl, about their own diameter apart, rising above well-defined spiral keels, and connected row to row by low axial ribs. The body whorl has 4 nearly equal rows of gemmules, the base is flattened and bears a smooth spiral keel. Aperture polygonal, slightly extended, the anterior spur sharply folded and reaching the columella, posterior canal a narrow V-shaped sinus. Columella column long, slightly oblique, tapering anteriorly to a rounded point. Length 8·6 mm.

Localities.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and two paratypes; 20 fm Lindeman Island (T. Iredale).

Remarks.—This species resembles *M. mellita* in general form, but is generally larger, the protoconch has a double instead of a single spiral keel, and the larger lower row of gemmules is distinctive. One of the paratypes, though apparently mature, is much smaller than the type, has only nine mature whorls, but is identical in all other characters. The Lindeman Island specimens, though geographically distant, are very close to the type.

Mesophora pallenta, sp. nov.

Figs. 44, 45, 66, and 67

Shell of medium size, conical, acuminate, spire slightly convex, colour brown to chocolate with the gemmules lighter or even quite white, worn specimens a uniform grey. Protoconch of 5 whorls, acuminate, with a single sharp spiral keel, crossed by very fine axial threads. Mature whorls 9, separated by distinct sutures. Sculpture at first 2 equal rows of smooth, rounded gemmules, 16–18 to the whorl, about half their diameter apart and rising above defined spiral keels, with thin axial connections. On the antepenultimate and penultimate whorls a median row of small gemmules develops, and on the body whorl there are 3 nearly equal rows, with a nearly smooth keel anterior to these, and 2 broad, smooth keels on the rounded base. Aperture round, expanded laterally and anteriorly, the anterior spur reaching the columella but not sharply folded, posterior canal a U-shaped sinus. Columella column short, slightly oblique, rounded anteriorly, with a plate of callus on the inner margin. Length 5·3 mm.

Localities.—7–10 fm Port Curtis (C. Hedley), holotype (Figs. 66 and 67); Port Curtis (J. Laseron), four paratypes; Hervey Bay (J. Laseron); Yeppoon (Mrs. M. Bowman) (Figs. 44 and 45); Murray Island.

Remarks.—In fresh specimens the white or light-coloured gemmules against a darker ground give this species a distinct facies which makes it easily recognized. Faded specimens are not uncommon in muddy areas in the Port Curtis district, and in this state can be confused with *M. bowenensis*, though they are uniformly smaller, have larger gemmules, and the sutures are more defined. The specimen from Murray Island, though from so far apart, is identical in every detail with the type.

Mesophora continens, sp. nov.

Figs. 68–71

Shell small, conical, spire very slightly convex, colour of type yellow-brown becoming white at the aperture, other specimens red-brown with the body whorl white. Protoconch conical, of 5 whorls, acuminate, the last 3 whorls with 2 spiral keels very close together, crossed by fine axial threads. Mature whorls 8, separated by deep sutures. Sculpture 2 main equal rows of gemmules, with a third small median row on the later whorls. The gemmules of the main rows are large and rounded, 14 to the whorl, about half their diameter apart, rising above well-defined spiral keels, and connected, row to row, by strong axial ribs. The body whorl has an additional small row anteriorly, and 2 smooth spiral keels on the base. Aperture expanded laterally and anteriorly with a nearly straight outer margin, the anterior spur sharply bent and reaching the columella, posterior canal a U-shaped sinus. Columella column nearly straight, rounded anteriorly. Length 4·2 mm.

Localities.—Darwin (J. Laseron), holotype (Figs. 68 and 69) and six paratypes; 15–20 fm off Point Charles, Darwin (M. Ward) (Figs. 70 and 71).

Remarks.—Though slightly variable in colour and size, this is a well-defined species, and characters to be noted are the deep sutures, large gemmules, and their strong spiral and axial connections. The dredged specimens are rather larger on the average than those from the shore.

Mesophora pura, sp. nov.

Figs. 72 and 73

Shell of medium size, elongate, conical, sides of spire nearly straight, colour pure white, protoconch and base faintly yellow. Protoconch conical, of 4 whorls, with a single sharp spiral keel crossed by axial threads, adult sculpture begininng abruptly. Mature whorls 10, sutures distinguishable but not deep. Sculpture 2 equal rows of gemmules, with a third median small row developing on the lower part of the spire, the gemmules of moderate size, rounded, close together, 18 to the whorl, neither the spiral nor axial connections well defined. Body whorl with 4 rows of gemmules, the uppermost the largest, with an additional smooth spiral keel on the base. Aperture rounded, not greatly expanded, the anterior spur sharply folded and reaching the columella to partly enclose the anterior canal, posterior canal a shallow round sinus. Length 6 mm.

Localities.—Lindeman Island (T. Iredale), holotype and 3 paratypes; 5–10 fm Hope Islands (C. Hedley).

Remarks.—The pure white colouration is a good guide to this species, and details of the form and sculpture also distinguish it from other members of the genus.

Mesophora sardonyx, sp. nov.

Figs. 74 and 75

Shell small, conical, spire slightly convex, a deep spiral band of chocolate covering the upper row of gemmules and the base, the lower row of gemmules cream. Protoconch small, conical, of 5 whorls, with a single keel overridden by axial threads. Mature whorls 7 in the type, 8 in some mature specimens, sutures not well defined. Sculpture 2 equal rows of gemmules on the first 3 whorls, a small median row appearing on the fourth and becoming larger on the later whorls. The gemmules are of medium size, about half their diameter apart, 16 to the whorl, the body whorl with an extra partially tuberculate keel anterior to the others and 2 smooth spiral keels on the rounded base. Aperture rounded, the outer margin reflected, the anterior spur reaching the columella, posterior canal a U-shaped sinus. Columella column short, straight, broad, rounded anteriorly, ridged on its inner margin. Length 3 mm.

Localities.—Under rocks, Bowen (J. Laseron), holotype and four paratypes; Barrier Reef off Cairns (D. Pitt), C.46022 in Australian Museum; Michaelmas Cay (T. Iredale); Darwin (J. Laseron).

Remarks.—Amongst species of *Mesophora* the colour pattern is striking and distinctive, though it resembles that of *Mastonia funebris* Jousseaume, except that the coloured band covers the upper and not the lower row of gemmules. Like that species also it has a wide range, and fragments have been recognized from many other localities. The holotype is rather smaller than most of the mature specimens, some of which attain a length of 5 mm.

Mesophora dolicha (Watson)

Figs. 76–79

Triforis dolicha Watson, 1886, p. 565, pl. 42, fig. 1.
Triphora tribulationis Hedley, 1909, p. 440, pl. 40, figs. 53 and 54.

The type locality is 28 fm west of Cape York, and Hedley's type came from the Hope Islands. Hedley also records his species from Masthead Island much farther to the south. Unfortunately specimens from the Hope Islands in the Australian Museum have deteriorated in the tubes and are unavailable for comparison, but specimens from Masthead Island agree with both Watson's and Hedley's figures and descriptions, and it is concluded that *tribulationis* is a synonym of *dolicha*. A specimen from Masthead Island is here figured (Figs. 76 and 77), its length being 4 mm, and another from Murray Island (C. Hedley) (Figs. 78 and 79), its length 5 mm. This differs by being larger, narrower, and with the columella column straight instead of sharply bent. Neither Hedley's nor Watson's figures show this character, and further material may show it to be a distinct species. A useful recognition point of this species is the colour which is cream with irregular patches of brown.

Mesophora aspergata, sp. nov.

Figs. 80 and 81

Shell of medium size, elongate, conical, with slightly convex sides, acuminate, protoconch white, remainder cream, with a broken band of brown between the gemmules. Protoconch slender, conical, of 5 whorls, the nucleus domed, the remainder with a single spiral keel overridden by fine axial threads. Mature whorls 11, sutures well defined. Sculpture 2 equal rows of rounded gemmules, 16 to the whorl, about half their diameter apart, rising above narrow spiral keels and connected axially by narrow ribs. On the last 3 whorls a median, narrow thread appears, which on the body whorl develops to a third row of gemmules, smaller than the other two. An additional anterior row is also present on the body whorl, and a small smooth spiral keel on the rather flattened base. Aperture rectangular, the outer margin nearly straight, expanded, in very mature specimens becoming subtubular and enclosing the anterior canal, posterior canal a deep narrow sinus which is widened and circular away from the margin. Columella column slightly oblique, rounded anteriorly. Length 5·6 mm.

Localities.—Barrier Reef off Cairns (D. Pitt), C.46011 in Australian Museum, holotype and two paratypes; Port Moresby (C. Hedley), C.8527, common; Bowen (J. Laseron); 17–20 fm Masthead Island (C. Hedley); Murray Island (C. Hedley).

Remarks.—The colouring makes this species very easy to recognize even in fragments, but otherwise it is very close to *M. pallenta*, previously described. Another closely allied species is *albocaelarea*, sp. nov., which is difficult to distinguish from *pallenta* particularly, but which has a protoconch with a double keel.

Mesophora albocaelarea, sp. nov.

Figs. 82 and 83

Size variable, from small to medium, conical with convex sides, swollen anteriorly, narrowed above, colour variegated, the general colour bright brown, with the gemmules lighter, the upper row often pure white, base and protoconch chocolate, with deep chocolate marking the spiral keels between the gemmules and to a lesser extent the sutures. Protoconch narrow, conical, of 5 whorls, a dome-shaped nucleus, the remainder with 2 spiral keels overridden by axial threads. Mature whorls 10, separated by defined sutures. Sculpture 2 rows of large, rounded gemmules, about their own distance apart, 13–14 to the whorl, rising from spiral keels, the rows well separated from each other, the space between occupied by a broken spiral cord, no axial connections distinguishable. This cord develops on the body whorl into a third row of gemmules, with an additional partly tuberculate keel anteriorly, and 2 plain spiral keels on the base. On the type the 2 main rows of gemmules are nearly equal, but on some specimens the upper row is distinctly larger. Aperture rounded, laterally expanded, the anterior spur sharply folded and reaching the columella, posterior canal a U-shaped sinus. Columella column short, nearly straight and truncate. Length of type 4·6 mm, another specimen 6 mm, others still larger.

Localities.—Bowen (J. Laseron), holotype and two paratypes; Curtis Island (J. Laseron), common; Yeppoon (Mrs. M. Bowman).

Remarks.—Except for deeper, more variegated colouring and slightly larger gemmules this species is very hard to separate from *M. pallenta*, but the critical difference is in the protoconch, *pallenta* having a single spiral keel, and *albocaelarea* a double one.

Mesophora rufosutura, sp. nov.

Figs. 84 and 85

Shell small, conical, spire convex, inflated anteriorly, narrowed posteriorly, colour cream, the upper row of gemmules white, sutures outlined by a narrow band of deep red-brown, protoconch and columella column brown. Protoconch conical and very slender, of 5 whorls, the nucleus domed, remainder with 2 spiral keels very close together, crossed by fine axial threads. Mature whorls 9, sutures deep and further defined by the coloured band. Sculpture 2 equal rows of large rounded gemmules, 16 to the whorl, close together, rising from defined spiral keels, the rows wide apart, connected axially by oblique ribs. These on the penultimate whorl rise into indistinct small gemmules, and on the body whorl they develop into a median row of small rounded gemmules. On the base are 2 more spiral keels, the upper partly tuberculate, the lower smooth. Aperture rounded, expanded, finally becoming subtubular, the anterior spur sharply folded, nearly enclosing the anterior canal, posterior canal narrow and deep, probably not quite fully developed in the type. Columella column long and tapering, very oblique, twisted almost at right angles to the axis of the spire, crossed by 2 rounded folds. Length 4·6 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype and two paratypes.

Remarks.—This species is clearly related to *pallenta*, *aspergata*, and *albocaelarea* and like the last has a protoconch with a double spiral keel. It can, however, be easily separated from all three by the distinctive colour pattern, and by the oblique, spur-like development of the columella column.

Mesophora calcara, sp. nov.

Figs. 86 and 87

Shell small to medium, elongate, irregularly conical, the lower part of the spire with very little taper and straight sides, the taper accentuated towards the apex, colour cream with pale, irregular, yellow-brown patches, columella yellow-brown. Protoconch conical, acuminate, of 6 whorls, the nucleus small, remaining whorls with a single, sharp spiral keel crossed by axial threads. Mature whorls 10, sutures deep. Sculpture 2 equal rows of gemmules on the earlier whorls, with a third median row developing on the later whorls, with a fourth row on the body whorl. The gemmules are large and round, close together, 14 to the whorl, rising above defined spiral keels, and connected axially by oblique ribs. There are 2 additional smooth spiral keels on the flattened base. Aperture rounded, anteriorly expanded, and becoming slightly tubular, the anterior spur sharply folded and reaching the columella, the posterior canal circular and open, distant from the margin, with which it is connected by a narrow slit. Columella column elongated, tapering and tubular, very oblique, twisted at right angles to the axis of the spire and upwards at its extremity. Length of holotype 5 mm, of another specimen 8 mm.

Localities.—15–20 fm off Point Charles, Darwin (M. Ward); holotype, Murray Island (C. Hedley).

Remarks.—In its colour pattern this species resembles both *M. torpedo*, sp. nov., and *M. dolicha* (Watson), but differs from both in its form, being less cylindrical than *torpedo* and having straighter sides than *dolicha*. Apart from details of sculpture the oblique, spur-like columella column is also even more exaggerated than in *dolicha*.

Mesophora albomicra, sp. nov.

Figs. 88 and 89

Shell small, conical, apex acuminate, spire with convex sides, slightly restricted at the base, colour a pure, uniform white. Protoconch conical, acuminate, continuing the line of the spire, of 5 whorls, with a single spiral keel and faint axial threads. Mature whorls 7, sutures not distinct. Sculpture 2 equal rows of gemmules, with a third small median row developing on the later whorls, the body whorl with an additional small anterior row and a single smooth spiral keel on the base. The gemmules are large, round, close together, 16 to the whorl, rising from ill-defined spiral keels and with obscure axial connections. Aperture small, round, expanded anteriorly, the anterior spur reaching the columella, the posterior canal a shallow sinus. Columella column short and broad, rounded anteriorly. Length 3·5 mm.

Localities.—Barrier Reef off Cairns (D. Pitt), holotype and four paratypes; 5–8 fm off Murray Island (C. Hedley); Michaelmas Cay (T. Iredale); 15–20 fm off Point Charles, Darwin (M. Ward).

Remarks.—The small size and pure white colour make this species easy to recognize. Its systematic position is open to doubt. The few whorls and small size suggest *Opimaphora*, but it is less inflated and restricted at the base than any species here referred to that genus. Its other characters agree well with *Mesophora*, and provisionally it is retained there. Of the specimens from Darwin, which are uncertainly placed here, one has a brown protoconch. Further material is needed to decide if more than one species or race is indicated.

Mesophora arafura, sp. nov.

Figs. 90 and 91

Shell of medium size, elongate, narrow, with nearly straight sides, acuminate, colour white, texture vitreous. Protoconch conical, slender, acuminate, of 6 whorls, with a single, sharp spiral keel, mature sculpture beginning abruptly. Mature whorls 10, separated by deep, narrow sutures. Sculpture 2 equal rows of medium-sized gemmules, 18 to the whorl, close together, rising from distinct spiral keels, the rows at first well apart and connected by axial ribs; these gradually break into a third median row of small gemmules, which on the body whorl are as large as the others. An additional row of small gemmules is anteriorly on the body whorl, and a smooth spiral keel on the flattened base. Aperture nearly rectangular, expanded anteriorly, the outer margin nearly straight, the anterior spur sharply bent but not reaching the columella, posterior canal a rounded sinus. Columella column nearly straight, broad, rounded anteriorly, a callus on the inner margin. Length 5·5 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and three paratypes.

Remarks.—The aperture of this species has not reached the stage of development shown by most species of the genus, but a longer series of specimens may show that fuller development may occur in older individuals. The very narrow form is distinctive. It is closest to *M. dolicha* (Watson), but is narrower, lacks the brown spots, differs in details of the sculpture, and has a straight columella column.

Genus CORIOPHORA, gen. nov.

Type species *Coriophora negrita*, sp. nov.

Small to medium-sized shells with the general characters, except the protoconch, very close to *Mesophora*, that is, the form is elongate with slightly convex sides, the sculpture begins as 2 rows of gemmules, a third row developing medially on the later whorls, the sutures are distinct, and the gemmules are spirally and axially connected. The aperture throughout is very close to *Mesophora*, and is of the twofold type, the true aperture in most species reaching the subtubular stage. In the few species in which the anterior canal is not completely enclosed, it is possible that longer series will show that further development takes place after maturity. The protoconch is, however, the determining character of the genus and the basis of its separation from *Mesophora*. It is not multiwhorled and slender as in *Mesophora* and lacks the sharp spiral keels and axial threads of that genus. In its most typical form it consists of a dome-shaped nucleus, more or less immersed in the summit, incipient or even mature sculpture immediately appearing on the next whorl. Or the 2 or 3 whorls following the nucleus may be nearly smooth, a single faint keel first developing, then a second, which gradually break into gemmules. Comparison may be made with *Isotriphora* Cotton & Godfrey (1931, p. 52), a southern Australian genus founded on the protoconch, the nucleus of which is quite immersed in the summit, with the early, fully sculptured whorls nearly planoid, making the whole apex domed.

Coriophora negrita, sp. nov.

Figs. 92 and 93

Shell small, narrow with a convex spire, slightly restricted at the base, colour a deep uniform red-brown, almost black. Apex blunt, protoconch of a broad, dome-shaped nucleus partially immersed in the summit, and overlapped by the first mature whorl, which is normally sculptured. Mature whorls 8, sutures barely distinguishable. Sculpture 2 rows of smooth rounded gemmules, elevated above narrow spiral keels and close together, 16 to the whorl, axial connections barely discernible. On the body whorl there are 4 rows and the gemmules are smaller and on the lower 3 rows ill defined. On the base are 2 additional smooth spiral keels. Aperture rounded, produced, and becoming subtubular, enclosing the anterior canal which opens within the aperture, posterior canal a deep U-shaped sinus. Columella column short and straight, truncate anteriorly. Length 4·8 mm.

Localities.—Port Curtis, 7–10 fm (T. Iredale), holotype and four paratypes; Capricorn Group (J. Laseron), common; Masthead Island (C. Hedley), common.

Remarks.—The form, colour, and blunt apex make this species easy to recognize. It varies somewhat in size, and the Capricorn specimens particularly fall into two groups otherwise indistinguishable, one group normal in size, the other smaller, averaging about 3·3 mm in length. Closely related to *negrita* is *mistura*, sp. nov., a species from Caloundra, which is lighter in colour and has a constantly different protoconch.

Coriophora marceda, sp. nov.

Figs. 94–97

Shell of medium size, conical, elongate, with convex sides, slightly restricted at the base, colour of type red-purple, the intensity varying on different rows of gemmules, in other specimens yellow-brown, but always with purple protoconch and a varying tinge of purple in some part. Protoconch short, a tilted nucleus, the next whorl slightly inflated with incipient keels, the next with 2 rounded keels gradually breaking into gemmules. Remaining whorls 11, sutures distinct but not deep. Sculpture on the early whorls 2 rows of gemmules, with a third small median row gradually developing. The gemmules are smooth and rounded, 20 to the whorl, close together, rising above low, broad spiral keels, and connected axially. The body whorl has 5 rows of gemmules, the upper large, the others small, and there is a thin, smooth spiral keel on the rounded base. Aperture rounded, expanded but not tubular, the anterior spur reaching the columella and covering but not completely enclosing the anterior canal; the posterior canal a V-shaped notch. Columella column short, oblique, posteriorly truncate. Length of holotype 5·8 mm, other specimens larger.

Localities.—Michaelmas Cay (T. Iredale), holotype and two paratypes (Figs. 94 and 95); Murray Island (C. Hedley), C.29478 in Australian Museum (Figs. 96 and 97), the specimen figured 7·5 mm long; Masthead Island (C. Hedley).

Remarks.—The red-purple colour may be a good guide to recognition, but even when the main colour is brown there is always some distinguishing tinge of purple. One of the Murray Island mature specimens is much smaller than that figured and has fewer whorls, but is otherwise indistinguishable. The Masthead Island specimens show the same variation, and are divisible into a large and small series.

Coriophora tigris, sp. nov.

Figs. 98–100

Shell of medium size, conical, spire slightly convex, slightly restricted at the base, apex purple, remainder with lower row of gemmules white, the other rows from yellow to red-brown. In other specimens the apex and the early whorls are white. Protoconch with a broad domed nucleus, mature sculpture beginning immediately on the next whorl. Whorls 11, separated by distinct but shallow sutures. Sculpture at first 2 rows of gemmules with a third small median row beginning about half-way down the spire. The gemmules number 16–18 to the whorl, rising above spiral keels and joined by low, rather indistinct, axial bars. The body whorl has 2 additional small rows of gemmules on the rounded base. Aperture rounded, anteriorly expanded but not tubular, the anterior spur crossing high on the columella and enclosing the

anterior canal, the posterior canal a deep V-shaped notch. Columella column short, oblique, and bent, rounded anteriorly. Length 5 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype and seven paratypes (Figs. 98 and 99); Barrier Reef off Cairns (D. Pitt), C.46019 in Australian Museum, Hayes Inlet, Moreton Bay (G. Gross), C.19200; Peel Island, Moreton Bay (Mrs. J. Kerslake), common (Fig. 100).

Remarks.—The banded colour pattern is a good recognition point for this species. In this it resembles *Mastonia funebris* Jousseaume, but that species has the lower row of gemmules coloured instead of the upper, and has quite a different protoconch. It is apparently widely distributed, though good material has been difficult to obtain, but broken specimens have been seen from a number of localities. The Moreton Bay specimens are generally larger and more robust than those from the Barrier Reef, and the colour band varies from yellow to deep chocolate. All lack protoconchs, but otherwise there is no appreciable difference. The one here figured for comparison is 7 mm long.

Coriophora fulva, sp. nov.

Figs. 101 and 102

Shell of medium size, conical, spire very slightly convex and slightly restricted at the base, colour a uniform bright yellow-brown. Apex blunt, protoconch short, a tilted, dome-shaped nucleus, followed by a slightly inflated whorl bearing a single spiral keel, mature sculpture appearing on the next whorl. Mature whorls 11, separated by shallow, indistinct sutures. Sculpture at first 2 equal rows of gemmules, with a thin median thread appearing about half-way down the spire, which gradually breaks into a third row of very small gemmules. The gemmules are relatively large, rounded, 16 to the whorl, close together, and rising above ill-defined spiral keels. On the body whorl the 3 rows of gemmules are nearly equal, and anteriorly there is an additional row and 2 nearly smooth spiral keels on the rounded base. Aperture thin and anteriorly expanded, the anterior spur reaching the columella and covering but not completely enclosing the anterior canal, posterior canal a deep U-shaped sinus. Columella column broad, slightly oblique, and rounded anteriorly. Length 5·2 mm.

Locality.—Murray Island (C. Hedley), C.29471 in Australian Museum, holotype and seven paratypes.

Remarks.—The colour again is here a good guide to the recognition of this species. From related species such as *C. marceda* (colour in part), it can be readily separated by the straighter spire and larger and fewer gemmules.

Coriophora nigrogranosa, sp. nov.

Figs. 103 and 104

Shell of medium size, conical, stout, with slightly convex sides, very slightly restricted at base, colour cream with small patches of brown covering the keels between the gemmules on both the upper and lower rows, the colour stronger on the lower whorls. Apex obtuse, a broad dome-shaped nucleus, the next 3 whorls nearly smooth, a faint single spiral keel developing, followed by a double one which gradually breaks into gemmules. Remaining whorls 10, the sutures narrow but distinct.

Sculpture on the earlier whorls 2, on the later whorls 3 rows of gemmules, the median row the smallest, the gemmules 18 to the whorl, rounded, about half their diameter apart, rising above defined spiral keels, and connected, row to row, by strong axial cords. Base of body whorl rounded, with 2 additional smooth, spiral keels. Aperture subquadrate, possibly not having reached its full maturity, the anterior spur not reaching the columella, leaving the anterior canal open, posterior canal a shallow sinus. Columella column short, bent, and oblique, anteriorly rounded, bordered by a ridge on the inner margin. Length 5·4 mm.

Locality.—Caloundra, holotype and one paratype.

Remarks.—The colouring and general appearance is almost exactly the same as *Mesophora aspergata*, previously described, and in the absence of the protoconch it is practically impossible to tell them apart. Some of the imperfect specimens from several localities tentatively placed in *aspergata* may well be this species. The protoconchs are, however, quite different, and when these are present there can be no doubt in identification. The aperture in the type is simple, but a long series will probably show that it attains the stage of most other members of the genus.

Coriophora intermissa, sp. nov.

Figs. 105–107

Shell of medium size, lower portion of spire cylindrical, tapering above, apex white, remainder straw, with patches of brown marking the spiral keels between the gemmules. Protoconch a single, tilted, dome-shaped nucleus partly immersed in the summit, the next 2 whorls with 2 prominent, rounded keels at the extreme top and bottom, these gradually breaking into gemmules. Whorls 13, sutures discernible but not deep. Sculpture 2 equal, widely separated rows of gemmules at the summit and base of the whorl, the gemmules small and rounded, alternating in adjacent rows, 16 to the whorl, about their own diameter apart, rising above low, narrow, spiral keels, but with no axial connections, the body whorl with 3 rows of gemmules, and a single low, broad, smooth spiral keel on the base. The base itself is hardly contracted and nearly continues the line of the spire. Aperture round, expanded anteriorly, and subtubular, entirely enclosing the anterior canal which opens within the aperture, the posterior canal circular, its rim raised but not tubular, connected with the outer margin of the aperture by a narrow slit. Columella column very short and broad, oblique, ridged on its inner and anterior margins. Length 5·3 mm.

Locality.—Capricorn Group (J. Laseron), holotype and three paratypes.

Remarks.—The colour pattern approaches that of *C. nigrogranosa*, but otherwise the form, sculpture, and protoconch are distinctive. The aperture also reaches the extreme of the twofold type, and a slightly greater development would make it threefold as in *Iniforis* and allied genera.

Coriophora monovitta, sp. nov.

Fig. 108

Shell of medium size, elongated, conical, becoming cylindrical in the later stage, colour yellow-brown, the lower row of gemmules nearly white, with the spiral keel between outlined in deep chocolate. Apex blunt, the protoconch in the holotype

rather worn, but apparently with a tilted, dome-shaped nucleus, followed by a single, rather inflated whorl. Remaining whorls 14, sutures well defined. Sculpture on the early whorls 2 equal rows of small gemmules, with a still smaller median row on the later whorls. The gemmules are rounded, 20 to the whorl, about their own diameter apart, rising above defined spiral keels, but with indistinct axial connections. The body whorl anteriorly has an additional partly tuberculate spiral keel, and the base is nearly flat. Aperture rounded, expanded anteriorly, subtubular, entirely enclosing the anterior canal, posterior canal a U-shaped sinus. Columella column tubular and oblique, quite open for the anterior canal at its extremity. Length 8 mm.

Localities.—Capricorn Group (J. Laseron), holotype; Michaelmas Cay (T. Iredale); Low Isles (T. Iredale).

Remarks.—Again this is a distinctive species, easily recognizable even in broken specimens by the small, numerous gemmules and the single, broken band of chocolate on the lower spiral keels. The aperture is of the advanced twofold type, and a longer series of specimens may prove that it becomes even further developed.

Coriophora claviculta, sp. nov.

Fig. 109

Shell small to medium in size, conical, spire slightly convex and restricted at the base, colour white to cream, all the gemmules a bright golden yellow, on the paratypes brown. Apex blunt, the protoconch of the type somewhat worn and details not discernible, but apparently it is short, conforming to the genus. Whorls 12, including the protoconch, sutures not deep but discernible. Sculpture 2 equal rows of medium-sized, rounded gemmules, 14 to the whorl, about their own diameter apart, the rows well separate at the bottom and top of the whorls, connected by spiral keels, but axial connections indistinct. The body whorl has an additional small anterior row of gemmules, and there is a plain spiral keel on the rounded base. Aperture rounded, anteriorly extended but not tubular, though it may not have reached its maximum development, the anterior spur reaching the columella and sharply folded, posterior canal a deep U-shaped sinus. Columella column straight, tapering slightly, and rounded anteriorly, crossed by several low folds. Length of type 4·5 mm, paratypes slightly larger.

Localities.—Barrier Reef off Cairns (D. Pitt), holotype and two paratypes; Michaelmas Cay (T. Iredale).

Remarks.—This is another very distinctive species. None of the specimens examined is in the finest condition, but the widely separated rows of gemmules, and the coloured gemmules against a white ground make even fragments easy to recognize. Its nearest relative is probably *Mastonia mediotincta* Hervier from Lifu.

Coriophora vermicula, sp. nov.

Figs. 110 and 111

Shell small, narrow, the lower portion cylindrical, the spire with nearly straight sides, apex blunt, the apex and early whorls white, remainder a uniform pale yellow. Protoconch short and cylindrical, the nucleus a slightly tilted dome, the next whorl

nearly smooth, followed by 2 whorls with very faint double spiral keels crossed by faint axial threads, only visible under strong magnification. Remaining whorls 9, parted by deep sutures. Sculpture 2 equal rows of gemmules, a median thread developing on the later whorls, which gradually breaks into a third row, distinct on the body whorl, which in addition has anteriorly another small row and a partly tuberculate spiral keel on the base. The gemmules are small, 16 to the whorl, about their own diameter apart, rising above well-defined spiral keels, axial connections obscure. Aperture rounded, extended, the anterior margin completely enclosing the anterior canal, the posterior canal a deep U-shaped sinus. Columella column short, broad, anteriorly truncate, slightly oblique. Length 3·8 mm.

Locality.—20 fm off Endeavour Reef (A. McCulloch), holotype.

Remarks.—This is the first of several small, rather inconspicuous species which need very careful microscopic examination for determination. The colour is here a good guide, as is the narrow, rather cylindrical form. The protoconch conforms to *Coriophora*, though extra whorls are developing with faint spiral and axial sculpture, but in no sense the multiwhorled aciculate protoconch characteristic of *Mastonia*, *Mesophora*, and some other genera.

Coriophora inconspicua, sp. nov.

Figs. 112 and 113

Shell small, conical, spire with slightly convex sides, apex blunt, colour of type nearly white with a pure white apex (may be faded), other specimens yellow to pale brown. Protoconch a dome-shaped nucleus, followed by 3 short whorls, appearing smooth under moderate magnification; but with a higher power a faint spiral keel is visible, with very faint axial threads near the base. Remaining whorls 10, parted by narrow, deep sutures. Sculpture 2 equal rows of gemmules, a third small median row developing on the later whorls. The body whorl has 3 rows, the anterior 2 small ones, with an additional nearly smooth spiral keel and a smooth spiral keel on the base. The gemmules are moderately large, close together, 16–18 to the whorl, rising above fine spiral keels, axial connections faint. Aperture rounded, extended, the anterior spur reaching the columella, the posterior canal a round orifice away from but connected to the outer margin of the aperture by a narrow slit. Columella column short, broad, straight, rounded anteriorly with a heavy plate of callus on the inner margin. Length 3·9 mm.

Locality.—Darwin (J. Laseron), holotype and three paratypes.

Remarks.—This is another small, inconspicuous species, differing from *C. vermicula* in form, by having larger and more closely set gemmules, and in details of the protoconch.

Coriophora mistura, sp. nov.

Figs. 114 and 115

Shell of medium size, elongate, apex blunt, spire slightly convex, colour a uniform yellow-brown. Protoconch short, slightly mammillate, with a small tilted nucleus, the next whorl inflated, with a faint spiral keel, the next whorl with 2 spiral keels breaking gradually into gemmules. Remaining whorls 9, separated by deep

sutures. Sculpture at first 2 equal rows of gemmules, a thin median spiral thread appearing about half-way down the spire and gradually breaking into a third row of small gemmules. The body whorl has 3 rows, the uppermost largest, with an additional partly tuberculate keel and 2 smooth spiral keels on the base. The gemmules are large, about half their own diameter apart, 16–18 to the whorl, rising above well-defined and elevated spiral keels, and axially connected by narrow ribs. Aperture simple, not reaching the stage of development of most members of the genus, rounded, the anterior spur reaching the columella, the posterior canal a V-shaped sinus. Columella column narrow, short, straight, rounded anteriorly, a heavy callus on the inner margin. Length 5 mm.

Localities.—Caloundra, holotype and one paratype; Peel Island, Moreton Bay (Mrs. J. Kerslake), common; Bowen (J. Laseron).

Remarks.—The Peel Island specimens all lack protoconchs, but otherwise conform closely to the type, except that some are larger, up to 8 mm in length. The specimens from Bowen are not quite mature, are slenderer and have a flatter spire, but conform in other characters including the protoconch. *C. mistura* is very close in many characters to *C. nigrogranosa* but is narrower, has smaller gemmules, and can easily be separated by the colour pattern.

Coriophora retusa, sp. nov.

Figs. 116 and 117

Shell of medium size, apex blunt, spire convex, broad, and tumid, restricted at the base, colour of protoconch white, remainder cream. Protoconch short and cylindrical, nucleus large, dome-shaped, and tilted, next 2 whorls with a single spiral keel and very faint axial threads. Remaining whorls 8, sutures indistinct. Sculpture 2 equal rows of moderately large gemmules, 16 to the whorl, about half their diameter apart, rising above weakly developed spiral keels, with no axial connections visible. On the penultimate whorl the lowest row of gemmules is the largest, with an incipient small median row which becomes a definite third row on the body whorl; this has another small anterior row and a further smooth spiral keel on the base. Aperture round, extended anteriorly and subtubular, the anterior spur crossing the columella high up and completely enclosing the anterior canal, posterior canal shallow but may not be fully developed. Columella column short, very oblique, medially bulbous. Length 5·7 mm.

Locality.—20 fm off Endeavour Reef (A. McCulloch), holotype and one paratype.

Remarks.—This is a distinctive species, in form approaching a *Mastonia*, from any species of which it can be readily separated by the short, stout protoconch.

Coriophora eximia, sp. nov.

Figs. 118 and 119

Shell of medium size, elongate, conical, spire only slightly convex, colour of apex white, remainder cream. Protoconch short, stout, cylindrical, apex large, the nucleus domed and tilted, the next whorl without visible sculpture, the second with 2 faint spiral keels developing. Remaining whorls 11, separated by deep,

well-defined sutures. Sculpture 2 equal rows of large, rounded gemmules, very close together, 20 to the whorl, a small median row gradually developing on the second half of the spire, the body whorl with 4 rows and another small row on the excavate base. Aperture round, slightly extended anteriorly, but may not be quite fully developed, the anterior spur sharply bent but not reaching the columella, the posterior canal not apparent. Columella column very short and broad, oblique and rounded, a heavy callus on the inner margin. Length 7·3 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype.

Remarks.—This species has a similar colour and protoconch to *C. retusa*, the preceding species, but it is larger, relatively narrower, and less convex, the sutures are deeper, the gemmules are more numerous and closer together, and the third median row develops earlier.

Coriophora montuosa, sp. nov.

Fig. 120

Shell of medium size, conical, spire with convex sides and slightly restricted at the base, colour of base and apex white, in the type the upper row of gemmules with a brownish tint, much stronger between the gemmules, in other specimens the upper row of gemmules yellow, the others white. Protoconch unknown. Remaining whorls 11, sutures not well defined. Sculpture 2 rows of large rounded gemmules, the lower row slightly larger, 14 to the whorl, rising from low, rounded spiral keels, axial connections not apparent, but a median undulating spiral thread on the lower whorls, the body whorl with an extra small anterior row of gemmules and a smooth spiral keel on the excavate base. Aperture rounded, anteriorly extended, the anterior spur reaching the columella, posterior canal a shallow sinus. Columella column short, oblique, broad, and rounded anteriorly.

Localities.—Michaelmas Cay (T. Iredale), holotype and one other specimen; Two Isles, off Cape Flattery (C. Hedley).

Remarks.—This species is doubtfully referred to *Coriophora* in the absence of the protoconch, but as it is nearest in other characters to *C. retusa* and *eximia* it may be left there until perfect material becomes available to decide the question. The colouration and the larger and fewer gemmules separate it from both those species.

Coriophora capricornia, sp. nov.

Figs. 121 and 122

Shell of medium size, robust, cylindro-conical, the last 3 whorls nearly equal, colour a uniform dull yellow-brown. Protoconch short, a tilted nucleus, the next whorl slightly inflated with an incipient keel, the following whorls with a single, then double, keel gradually breaking into gemmules. Remaining whorls 9, separated by narrow but deep sutures. Sculpture at first 2 rows of gemmules, the upper row the larger, a third small median row appearing about one-third down the spire, becoming progressively larger, the body whorl with an extra row anteriorly, and a small, smooth spiral keel on the base. The gemmules are small and closely packed, 22 to the whorl, rising above well-defined keels, irregular and nearly square in shape, and connected axially by narrow cords. Aperture rounded, the margins thin and

reflected, the anterior spur reaching the columella and covering the anterior canal, posterior canal a shallow sinus. Columella column broad, slightly oblique and truncate anteriorly. Length 6·2 mm.

Locality.—Capricorn Group (J. Laseron), alive under coral boulders, holotype and five paratypes.

Remarks.—Among species of *Coriophora* the sculpture alone makes this species distinctive, but in both colour and sculpture it is so close to *Mesophora pavimenta* described earlier that in the absence of the protoconch it is practically impossible to distinguish between them. The difference in the protoconch is, however, fundamental, and given perfect material there should be no difficulty in identification.

Coriophora tubularis, sp. nov.

Figs. 123 and 124

Shell of medium size, elongate, narrow, lower two-thirds of spire cylindrical, upper third with only a slight taper, colour a uniform purple, the apex pale. Protoconch short and broad, a large dome-shaped, slightly tilted nucleus, the next whorl nearly smooth, 2 faint spiral keels appearing on the second whorl. Total whorls 12, separated by narrow, channelled sutures. Sculpture at first 2, and then 3 rows of gemmules, the median row smaller, but in the antepenultimate and penultimate whorls nearly as large as the others. The body whorl has an additional anterior row of gemmules and a smooth spiral keel on the slightly rounded base. The gemmules are small, 18 to the whorl, rounded and smooth, about half their diameter apart, rising from well-defined spiral keels, and connected axially by strong cords. Aperture slightly expanded laterally and anteriorly, the anterior spur sharply bent and just reaching the columella, the posterior canal a V-shaped notch right on the suture. Columella column short, straight, broad, crossed by a strong fold, rounded anteriorly. Length 5·2 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype and five paratypes.

Remarks.—This is a well-marked species, one of the few with a uniform purple colour. There is no other species of *Coriophora* with which it can readily be confused, but in form it is close to *Mesophora torpedo* previously described, from which it can be readily distinguished by the colour, and generically by the protoconch.

Genus SUBULOPHORA, gen. nov.

Type species *Subulophora exporrecta*, sp. nov.

Subulophora is proposed for a group of long, attenuate shells with straight sides, with multi-whorled protoconchs similar to *Mesophora* and similar sculpture except that there is nearly always one row of gemmules larger than the others. The apertures in the species observed have not reached the stage of development of such genera as *Mastonia*, *Mesophora*, and *Coriophora*, and can be classed as simple, the outer margin thin and often polygonal, the anterior spur reaching the columella, the posterior canal a shallow sinus.

Several species are described here with these characteristics, but it is probable that others exist in northern waters. The shells are easily broken and fragments which are specifically indeterminable have been seen from a number of localities.

Subulophora exporrecta, sp. nov.

Figs. 125 and 126

Shell of medium size, cylindrical, elongate, and narrow, spire with straight sides, protoconch brown, remainder pale straw. Protoconch conical and acuminate, of 6 whorls, nucleus small, other whorls with 2 sharp spiral keels overridden by strong axial threads. Mature whorls about 16, sutures ill defined and difficult to detect. Sculpture on early whorls 2, on later whorls 3 rows of gemmules, the median row small, the others equal, the gemmules round, about half their diameter apart, 16 to the whorl, rising above well-defined spiral keels, but with indistinct axial connections. The body whorl has an extra anterior row of gemmules, and a small smooth spiral keel on the flattened base. Aperture round, the outer margin widely reflected, anterior spur just reaching the columella, posterior canal a V-shaped sinus. Columella column nearly straight, rounded anteriorly, a thick plate of callus on the inner margin. Length 7 mm.

Locality.—Port Moresby (C. Hedley), C.8525 in Australian Museum, holotype and one paratype.

Remarks.—There is no other known species with which this can readily be compared, the sculpture distinguishing it from other long attenuate species assigned to other genera. It is probably not rare, as fragments have been seen from other localities which may well be this species.

Subulophora strigosa, sp. nov.

Figs. 127–129

Shell small, conical, elongate, attenuate, with nearly straight sides, colour uniform, varying from a pale cream to pale brown. Protoconch slender, long and acuminate, of 7 whorls, a small nucleus, remainder with a sharp single spiral keel crossed by fine axial threads. Mature whorls in the type 11, but occasionally fewer, sutures moderately deep. Sculpture in the earlier whorls 2 rows of gemmules which are at first nearly equal, in the later whorls 3 rows of which the lowest is much the largest, the rows close together with indistinct axial connections. The gemmules are rounded, close together, 16 to the whorl, the body whorl with an extra anterior row and a smooth spiral keel on the flattened base. Aperture rounded, anteriorly expanded, the anterior spur reaching the columella, the posterior canal a V-shaped sinus. Columella column oblique, rounded anteriorly. Length 4·7 mm.

Localities.—5–8 fm Murray Island (C. Hedley), holotype (Figs. 127 and 128) and two paratypes; 5–10 fm Hope Islands (C. Hedley), C.27317 in Australian Museum, common (Fig. 129); Mornington Island (C. Hedley), C.14601; 17–20 fm Masthead Island (C. Hedley), C.13590; Darwin (J. Laseron), from beach; 15–20 fm Point Charles, Darwin (M. Ward).

Remarks.—This is a not uncommon and widely spread species, easily recognizable by its very narrow form, long protoconch, and the enlargement of the lower row of gemmules. It is generally constant, though odd specimens have been noticed which attain maturity at a much earlier stage, and thus have fewer whorls. This is particularly noticeable in the series from the Hope Islands, and in the smaller

specimens the inequality in size of the rows of gemmules is not nearly so marked. One of these is figured for comparison (Fig. 129). It is only 3 mm long, and has only six mature whorls, actually less than in the protoconch, which thus is relatively very large.

Subulophora minima, sp. nov.

Figs. 130 and 131

Shell small, slender and acuminate, the spire with nearly straight sides, colour of apex white, remainder a uniform yellow-brown. Protoconch broadly conical, the taper more rapid than that of the main spire, acuminate, of 5 whorls, the apex minute, the whorls short, the first 2 rounded, a slight spiral keel forming on the third, and only on the last 2 becoming prominent and sharp with axial threads. Mature whorls 9, sutures distinct and channelled. Sculpture of 2 rows of gemmules, the lower distinctly the larger, with a third small median row developing on the later whorls, the body whorl with 3 rows of gemmules and 2 additional smooth spiral keels on the base. The gemmules are round, about half their diameter apart, 13 to the whorl, rising above defined spiral keels, alternate on the top and bottom rows, axial connections indistinct. Aperture rounded, extended, the anterior spur reaching the columella, the posterior canal a deep, V-shaped sinus. Columella column short, slightly oblique, rounded anteriorly, a heavy callus on the inner margin. Length 3·8 mm.

Locality.—Darwin (J. Laseron), holotype and seven paratypes.

Remarks.—This species greatly resembles *S. strigosa*, but in the type locality where both species occur, it was readily separated by its white apex, by being uniformly smaller and by details of the sculpture. The main difference is, however, in the protoconch, which in *strigosa* is broader, has fewer whorls, and the spiral keel and axial threads are only apparent on the last two whorls.

Subulophora whitleyi, sp. nov.

Figs. 132 and 133

Shell small, regularly conical with straight sides, slender and attenuate, colour a uniform yellow. Protoconch relatively large, conical, its angle of taper more obtuse than that of the main spire, of 7 whorls, the nucleus small, the remainder with a single sharp keel and numerous strong axial threads. Mature whorls 11, sutures difficult to distinguish from the channels between the gemmule rows. Sculpture in the early whorls 2 equal rows of gemmules, with a third small median row developing on the later whorls, increasing to the same size as the others on the body whorl, which also has a partly tuberculate keel, and 2 small smooth spiral keels on the rounded base. The gemmules number 14 to the whorl, rise above defined spiral keels, are slightly elongated in a spiral direction, and no axial connections were noted. Aperture rounded, laterally expanded, the anterior spur barely reaching the columella, the posterior canal a deep, narrow U-shaped notch with parallel sides. Columella pillar long, curved, and oblique, inner margin with a heavy callus. Length 5 mm.

Locality.—Cambridge Gulf, north-west Australia (G. Whitley), holotype and three paratypes, dredged.

Remarks.—A small parcel of dredgings has yielded two Triphoridae species from this locality, the first recorded from the far north-west, though undoubtedly it only needs keen collecting to reveal many more. *S. whitleyi* can readily be separated from the nearest Australian species, *S. strigosa*, by the equal rows of gemmules, the spiral elongation of the gemmules, and the long oblique columella column. It is even nearer to *S. indianica*, a species described from Christmas Island in the Indian Ocean in a later Section of this paper, but that species has a protoconch with a double spiral keel and a straighter columella column.

Genus DISTOPHORA, gen. nov.

Type species *Distophora distorta*, sp. nov.

Shell long, slender, cylindrical, of rather irregular growth, apex blunt, the protoconch a single large dome-shaped nucleus, aperture simple, sutures not channelled, sculpture of 3 spiral keels, the middle the largest, broken into closely packed, irregular gemmules.

This genus is proposed for a single, somewhat aberrant species which will not fit into any other of the genera here used. The nearest relation may be *Aclophora*, gen. nov., from which it can be distinguished by the slender, cylindrical form, the inequality of the keels and the ill-defined gemmules.

Distophora distorta, sp. nov.

Figs. 134 and 135

Shell of medium size, slender, elongate, spire nearly cylindrical, with a very slight taper, apex blunt, colour white, with a few small irregular patches of yellow. Protoconch a single, large, dome-shaped nucleus right on the summit, sculpture beginning on the next whorl as 3 rounded keels which gradually break into irregular gemmules. Whorls 12, separated by barely distinguishable sutures. Sculpture 3 broad spiral keels, separated by narrow channels, the middle keel the largest, broken into numerous, closely packed, ill-defined and irregular gemmules, about 20 to the whorl, the slightest wear making the keels appear almost smooth, 2 smaller additional keels on the base of the body whorl. Aperture of simple type, the anterior spur barely developed and not reaching the columella, posterior canal a very shallow sinus. Columella column straight, smooth, rounded anteriorly. Length 6·5 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype (Fig. 134) and seven paratypes; Murray Island (C. Hedley).

Remarks.—Apart from the distinctive characters given in the specific description a feature in about half the paratypes is a curious distortion which affects the later whorls. This appears as a sudden enlargement to as much as twice the diameter, and may be in the body whorl only or in the last three whorls. A specimen from Murray Island, not quite mature, 5 mm in length, showing this distortion is here figured (Fig. 135). The cause of the distortion and whether it has any specific significance is not known.

Genus NANAPHORA, gen. nov.

Type species *Nanaphora torquesa*, sp. nov.

Nanaphora is proposed for a large group of small or even minute shells, all bottle-shaped, medially inflated, and restricted at the base, with relatively few whorls, generally under 10. All have blunt apices, sometimes mammillate, protoconchs of not more than 2 or 3 whorls, often a single, broad, dome-shaped nucleus immersed in the summit, incipient mature sculpture appearing early as rounded spiral keels, gradually breaking into gemmules. The aperture is generally beyond the simplest form, the true aperture after maturity in most species becoming subtubular and enclosing the anterior canal, but the posterior canal does not develop beyond a deep sinus and does not form a circular orifice. Sculpture is typically of 2 rows of rounded gemmules, with the sutures just distinguishable but not channelled, but a third median row of small gemmules sometimes appears on the later whorls.

Within this description a number of tropical species can be readily assigned, but a few others which are slightly divergent in character may subsequently need separation into a different genus or genera. Other small, inflated shells, which have a different, multi-whorled protoconch, are later proposed as another genus, *Opimaphora*. In both groups a useful guide to specific determination is colour which appears to be specifically constant.

NANAPHORA TORQUESA, sp. nov.

Figs. 136 and 137

Shell small, bottle-shaped, upper portion of spire slender, medially greatly inflated, restricted at the base, colour of apex and earlier whorls pure white, 2 rows of gemmules on the shoulder of the spire yellow-brown, the remainder a uniform pale straw. Apex mammilate, protoconch with a very small tilted nucleus, the next whorl inflated with axial cords, the second whorl shorter with a single spiral keel, breaking into incipient gemmules. Remaining whorls about 7, sutures indistinguishable. Sculpture 2 rows of large rounded gemmules, 14 to the whorl, becoming smaller on the restricted base, about their own diameter apart, rising above narrow spiral keels, and connected axially by low rounded bars, base of body whorl rounded with 2 extral small smooth spiral keels. Aperture rounded, subtubular, extended anteriorly, completely enclosing the anterior canal which opens within the aperture, posterior canal a U-shaped sinus. Columella column short, curved, and very oblique. Length 4 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype and one paratype; 5–8 fm off Murray Island (C. Hedley).

Remarks.—The form, protoconch, sculpture, and colour band should afford ready recognition of this striking little species. The paratype is rather larger than the holotype and is 5·6 mm in length with the lower portion of the spire nearly cylindrical, but it conforms in all other characters. The Murray Island specimen is rather doubtfully assigned here as it lacks the colour band and is pure white.

Nanaphora projecta, sp. nov.

Fig. 138

Shell small, bottle-shaped, narrow towards the summit, medially inflated, restricted at the base, the apex and next 3 whorls pure white, the next whorl pale ochre, the last 3 whorls straw with the lower row of gemmules ochre, the base ochre. Apex mammillate, the nucleus small and tilted, the next whorl inflated, incipient sculpture appearing on the second whorl. Remaining whorls 7, sutures narrow and distinct. Sculpture of 3 rows of very large gemmules, the rows almost touching and the gemmules very close together, 14 to the whorl, the body whorl with 4 rows of gemmules and a small smooth spiral keel on the flat base. Aperture semicircular, subtubular, expanded anteriorly, covering the anterior canal which opens within the aperture, the posterior canal a U-shaped sinus. Columella column narrow, curved, oblique. Length 4·1 mm.

Locality.—5–8 fm off Murray Island (C. Hedley), C.48640 in Australian Museum, holotype and three paratypes.

Remarks.—This is another distinctive species, readily separable from *N. torquesa* by the colour pattern, by being less inflated, and by the more defined sutures and sculpture. The sculpture alone suggests that it should be separated generically, but as none of these small inflated species has been studied from seas outside Australia, it is considered that until this is done a more comprehensive classification should be deferred.

Nanaphora rufozonata, sp. nov.

Figs. 139 and 140

Shell small, bottle-shaped but comparatively narrow, restricted at the base, colour of apical whorls yellow, the next 2 whorls pure white, remaining whorls pale brownish yellow, sutures and base red-brown, columella column amber. Apex narrow but not acuminate, cylindrical, the nucleus tilted, the next 2 whorls without discernible sculpture, incipient sculpture appearing on the third whorl. Remaining whorls 7, sutures distinct. Sculpture 2 equal rows of gemmules, 15–16 to the whorl, close together, without distinct spiral or axial connections, the gemmules rounded, but on the penultimate whorl the upper row becomes much larger and axially elongated, on the body whorl finally splitting into 2 rows by the division of the gemmules themselves. In addition there are 2 extra rows on the base. Aperture rounded, in the holotype not produced into a tube, the anterior spur not reaching the columella, but bent sharply to flank a narrow, open anterior canal, posterior canal a deep, narrow slit. Columella column straight, anteriorly rounded, a callus on the inner margin. Length 4·2 mm.

Locality.—Barrier Reef off Cairns (D. Pitt), holotype, C.46015 in Australian Museum.

Remarks.—The distinctive colour pattern, form, and sculpture distinguish this from the species already described.

Nanaphora murrayensis, sp. nov.

Figs. 141 and 142

Shell small, bottle-shaped, tumid, restricted at the base, the apical and early whorls pure white, the last 4 whorls and base a uniform yellow-brown. Apex blunt, the nucleus dome-shaped, 2 spiral keels developing on the next whorl with faint axial threads which gradually break into gemmules. Remaining whorls 8, sutures barely distinguishable. Sculpture on the early whorls 2 equal rows of small rounded gemmules, about 20 to the whorl, about half their diameter apart, rising above spiral keels. On the median whorls these rows are well apart and are connected axially by narrow ribs. On the penultimate whorl a median spiral cord develops which gradually breaks into a row of small gemmules. The body whorl has 4 rows, the gemmules on the 3 lower rows becoming indistinct, and there is a further thin smooth spiral keel on the base. Aperture in the type not quite perfect, the outer margin being broken, but the anterior spur apparently barely reaches the columella. Columella column broad, straight, and anteriorly truncate, Length 3·8 mm.

Locality.—5–8 fm Murray Island (C. Hedley), holotype.

Remarks.—This species is very close in colour and sculpture to *N. cylindrica*, later described, but is broader, has quite a different contour, and the broad, truncate columella column at once distinguishes it.

Nanaphora cylindrica, sp. nov.

Figs. 143 and 144

Shell small, slender above, becoming nearly cylindrical in lower portion of spire, the last 3 whorls nearly equal, slightly restricted at the base, colour of apex and the next 3 whorls pure white, remainder red-brown. Protoconch short and mammillate, a large tilted nucleus, followed by an inflated whorl with 2 very faint spiral keels gradually breaking into gemmules. Remaining whorls 8, sutures not well defined. Sculpture at first 2 equal rows of gemmules, with a third small median row developing half-way down the spire, the body whorl with 4 rows, the upper larger than the others, and with 2 small smooth spiral keels on the base. The gemmules are comparatively large, close together, 18 to the whorl, rising above spiral keels and connected axially by narrow bars. Aperture rounded, not subtubular, the anterior spur reaching the columella and enclosing the anterior canal, the outer margin in the type not quite perfect and not showing the anal notch. Columella column long, nearly straight, and rounded anteriorly. Length 3·6 mm.

Localities.—5–8 fm Murray Island (C. Hedley), holotype (Fig. 143); 17–20 fm Masthead Island (C. Hedley); Bustard Head (Miss G. Thornley); Heron Island (Miss B. Dew) (Fig. 144).

Remarks.—The colour and nearly cylindrical form distinguish this from species previously discussed, though in these characters it is close to *N. truncis* next described. A single specimen from Heron Island, 4·6 mm in length, does not quite conform to the type, and further material may show it to be a distinct species. It is here figured

for reference (Fig. 144). It is larger and has a white top, but the remainder is yellow and not red-brown, the gemmules are more closely packed, and the protoconch is slightly different.

Nanaphora truncis, sp. nov.

Fig. 145

Shell small to medium in size, stout, the main portion of spire perfectly cylindrical, the last 5 whorls practically equal, tapering rapidly at the apex, slightly restricted at the base, colour a uniform deep chocolate, almost black, the summit yellow. Protoconch unknown. Type with 10 whorls, sutures distinct but not deep. Sculpture on the early whorls 2 equal rows of gemmules with a third small median row developing on the later whorls, the body whorl with the uppermost row largest, the next 2 equal, with an additional, partly tuberculate spiral keel anterior to these, and 2 smooth spiral keels on the base. The gemmules are of medium size, rounded, 18 to the whorl, about half their diameter apart, rising from distinct spiral keels and with slender but distinct axial connections. Aperture in the type not fully developed, but other specimens show it to be subtubular, completely enclosing the anterior canal, the posterior canal a deep narrow slit. Columella column very short, very broad, and rounded. Length of type 6 mm, but some specimens are little more than half this.

Localities.—Capricorn Group (J. Laseron), holotype and two small specimens; Barrier Reef off Cairns (D. Pitt), one small specimen; Low Isles (T. Iredale), two specimens similar to type.

Remarks.—The perfect cylindrical form, deep colouring, and aperture distinguish this from *N. cylindrica* and make even fragments easy to recognize. Specimens fall into two series by size, but there are no other differences, and the difference in size may possibly be sexual.

Nanaphora melwardi, sp. nov.

Fig. 146

Shell small, with a flattened apex, the spire convex, slightly inflated in the lower portion and restricted at the base, the apex and earlier whorls pure white, remainder pale yellow. Protoconch a flattened dome above a sharp spiral keel, the next whorl with a single spiral keel, sculpture beginning gradually on the following whorl. Remaining whorls 8, sutures distinct. Sculpture 2 equal rows of gemmules, with a third small median row developing on the later whorls, the body whorl with a larger upper row, 3 smaller rows, and 2 small smooth spiral keels on the base. The gemmules are rounded, of intermediate size, 18 to the whorl, rising above defined spiral keels, and connected axially by narrow ribs. Aperture rounded, expanded anteriorly, the anterior spur reaching the columella, the posterior canal a deep U-shaped sinus. Columella column oblique, narrowed and truncate anteriorly. Length 4 mm.

Locality.—10–20 fm off Point Charles, Darwin (M. Ward), holotype and one paratype.

Remarks.—This species resembles *N. cylindrica* in many characters, but has a much paler colour, a different contour, and above all the peculiar cap-shaped protoconch is distinctive.

Nanaphora caloundra, sp. nov.

Figs. 147 and 148

Shell small, solid, broad with a convex spire, restricted at the base, colour uniformly yellow. Apex tumid, protoconch short, nucleus broad and dome-shaped, the following whorl with a single spiral keel crossed by axial cords. Remaining whorls 6, sutures defined. Sculpture 2 rows of smooth rounded gemmules, without apparent spiral or axial connections, 16 to the whorl. Between these rows a spiral thread appears on the antepenultimate whorl, which on the body whorl breaks into an extra row of gemmules, while the anterior row decreases in size. Anterior to this are 2 more smooth spiral keels. Aperture with a thin sinuous outer margin, rounded anteriorly, the anterior spur not sharply bent and not reaching the columella, leaving the short anterior canal quite open, posterior canal a shallow rounded sinus. Columella column short, straight, rounded anteriorly. Length 3·1 mm.

Locality.—Caloundra, holotype and nine paratypes.

Remarks.—This species is doubtfully referred to *Nanaphora*, as in all the specimens examined the aperture is of simple type and shows no tendency to become tubular after maturity. In this it resembles some of the southern temperate species such as *labiata* Adams, and it may later be necessary to introduce still another genus to include such forms.

Nanaphora mamilla, sp. nov.

Figs. 149 and 150

Shell small, stout, apex blunt, spire convex, swollen in lower portion of spire and slightly restricted anteriorly, colour a uniform creamy white. Protoconch small, flatly coiled, and just showing above the summit, with a single obscure spiral keel. Remaining whorls 8, sutures distinguishable but not deep. Sculpture 2 equal rows of large rounded gemmules, close together, 18 to the whorl, the connecting keels faint, the rows well apart and connected by axial ribs, the body whorl with a large upper row of gemmules and 3 smaller anterior rows, a smooth spiral keel on the base. Aperture rounded, laterally and anteriorly expanded, the anterior spur sharply bent and reaching the columella, the posterior canal a deep U-shaped sinus. Columella column oblique, rounded anteriorly, a thick plate of callus on the inner margin. Length 3·5 mm.

Locality.—20 fm off Endeavour Reef (A. McCulloch), holotype and one paratype.

Remarks.—In form this resembles *N. caloundra*, but differs in details of the protoconch, sculpture, and the aperture.

Nanaphora tricolor, sp. nov.

Figs. 151 and 152

Shell small, very inflated, spire regularly convex, restricted at the base, apex mucronate, white, remainder with upper row of gemmules white, lower row deep

chocolate, the intermediate groove or median row of gemmules and base yellow. Protoconch of type broken, but from a Caloundra immature specimen it is seen to be mucronate (Fig. 152), the nucleus broad and dome-shaped, the next 2 whorls with 2 ill-defined spiral keels, gradually breaking into gemmules. Remaining whorls 8, short, separated by deep sutures. Sculpture on early whorls 2 equal rows of smooth rounded gemmules, 20 to the whorl, close together, rising from low indistinct spiral keels, with a third small median row on the later whorls, the body whorl with 2 extra rows of small gemmules on the rounded base. Aperture imperfect, but apparently of simple type, with the anterior spur not reaching the columella. Columella column short, broad, straight, rounded anteriorly, crossed by a prominent fold. Length 4 mm.

Localities.—Angowrie, near Clarence River, New South Wales (A. A. Cameron), holotype; Caloundra, a number of imperfect specimens.

Remarks.—Though the holotype comes from a Peronian locality, it has a tropical facies, and as the species is not uncommon at Caloundra, it is obviously one of the many tropical migrants which have invaded northern New South Wales. It is described from not quite perfect material, but the distinctive colour pattern makes the recognition of even fragments easy, and there should be no trouble in its future identification.

Genus OPIMAPHORA, gen. nov.

Type species *Opimaphora sarcira*, sp. nov.

Small shells with under 10 mature whorls, medially greatly inflated, with acute apices, restricted anteriorly. Protoconchs acuminate of several whorls, bearing single or double spiral keels, crossed by axial threads or cords. Sutures not defined, sculpture of 2 rows of gemmules with sometimes a small third median row on the penultimate and body whorls. Aperture small, of the twofold type, the true aperture becoming tubular after maturity, the anterior canal opening within the aperture, the posterior canal generally a rounded orifice, but opening to the margin of the aperture and not tubular.

This seems a natural group, all tropical in habitat, distinguishable from *Nanaphora* mainly by the multi-whorled slender protoconch. From *Mastonia* the genus can be distinguished by the small, greatly inflated shell and by the fewer mature whorls, invariably under 10.

Opimaphora albescens, sp. nov.

Figs. 153 and 154

Shell small, bottle-shaped, medially very inflated, restricted anteriorly, colour a uniform creamy white. Protoconch conical, of 4 whorls, the nucleus domed, remainder with 2 rounded keels, gradually breaking into gemmules. Mature whorls 6, the sutures not defined. Sculpture of 2 rows of large rounded gemmules, 16 to the whorl, nearly touching each other both spirally and axially, an intermediate smaller row on the body whorl with another still smaller row anteriorly and a small, smooth spiral keel on the base. Aperture polygonal, expanded, and subtubular, entirely enclosing the anterior canal which opens within the aperture, posterior canal

a round sinus. Columella column short, slightly oblique, and rounded anteriorly. Length 2·8 mm.

Locality.—5–8 fm Murray Island (C. Hedley), holotype and one paratype.

Remarks.—There is no other previously described species with which this can be readily compared. Its general characters are sufficiently distinctive to make its future recognition relatively easy. The protoconchs of both *O. albescens* and *O. inflata*, the next species described, do not quite conform to the generic description, as while both are multi-whorled, the spiral keels are not sharp and the fine axial threads are absent. It is possible that their relationship may ultimately be found to be closer to *Nanaphora* than *Opimaphora*.

Opimaphora inflata, sp. nov.

Figs. 155 and 156

Shell small, bottle-shaped, very inflated and restricted anteriorly, protoconch yellow-brown, the next 2 whorls pure white, remainder deep chocolate, edge of columella and aperture white. Protoconch narrow and cylindrical, of 4 whorls, the nucleus domed, the other whorls with two narrow spiral keels gradually breaking into gemmules. Mature whorls 6, sutures not distinct. Sculpture on the first 4 whorls 2 equal rows of large, smoothly rounded gemmules, 18 to the whorl, about half their diameter apart, rising above spiral keels, the penultimate and body whorls with a small median row of gemmules, the body whorl with another small row anteriorly and a thin smooth spiral keel on the base. Aperture rounded, subtubular, with thin margins, completely enclosing the anterior canal which opens within the aperture, the posterior canal a rounded sinus. Columella column short, oblique, and truncate anteriorly. Length 3·3 mm.

Localities.—Port Moresby (C. Hedley), C.8531 in Australian Museum, holotype; 20 fm off Endeavour Reef (A. McCulloch).

Remarks.—The short obese form and colour pattern are distinctive, otherwise it is close to *O. albescens*, but differs also in details of the sculpture.

Opimaphora sarcira, sp. nov.

Figs. 157 and 158

Shell small, medially inflated, restricted at the base, apex acuminate, protoconch deep brown, remainder cream with irregular deep chocolate patches, base brown. Protoconch conical, of 4 whorls, with a single sharp spiral keel, crossed by fine axial threads, mature sculpture beginning abruptly. Mature whorls 7, sutures not defined; sculpture 2 rows of large rounded gemmules, close together both spirally and axially, 16 to the whorl, the body whorl with 3 extra small rows on the base. Aperture rounded, extended, and subtubular, the anterior canal entirely enclosed and opening within the aperture, posterior canal nearly enclosed, circular, open to the outer margin by a narrow slit. Columella column very short, oblique, broad, and rounded anteriorly. Length 3·2 mm.

Localities.—Capricorn Group (J. Laseron), holotype; Barrier Reef off Cairns (D. Pitt), C.46010 in Australian Museum; Low Isles (T. Iredale).

Remarks.—*O. sarcira* has been chosen as the type of the genus, as it is considered that the form, sculpture, and particularly the protoconch and aperture are the critical factors to be considered if any further generic revision is done in the future. From all other species of *Opimaphora* here described it can be readily separated by its distinctive colour pattern, which is, however, also found in other groups. The several specimens from off Cairns differ slightly by all having white protoconchs and the colour patches paler, but they may be faded. *Mastonia turricula* Hervier from Lifu resembles *sarcira* in colour, is also small and inflated, but has a different contour.

Opimaphora albogemmata, sp. nov.

Figs. 159–161

Shell small and bottle-shaped, apex acuminate, medially greatly inflated, and much restricted at the base; protoconch and early whorls yellow, remainder almost black, the gemmules white. Protoconch slender and cylindrical, of 5 whorls, the last 3 with a double spiral keel which gradually breaks into gemmules. Remaining whorls 7, the sutures not defined. Sculpture 2 rows of large, rounded gemmules, close together both spirally and axially, 15–16 to the whorl, the body whorl with 3 rows becoming progressively smaller, with 2 additional partly tuberculate spiral keels on the base, and another smooth spiral keel just above the columella column. Aperture relatively small, rounded, extended, and subtubular, but not quite enclosing the anterior canal, the posterior canal a circular orifice connected by a narrow slit with the outer margin of the aperture. Columella column very short and broad, rounded anteriorly. Length 3·6 mm.

Localities.—Capricorn Group (J. Laseron), holotype and two paratypes; Masthead Reef (C. Hedley), C.19034 in Australian Museum; Michaelmas Cay (T. Iredale).

Remarks.—Again the colour pattern is a good guide to recognition, and the very obese form and short columella column are other distinctive characters. The single specimen from Michaelmas Cay is doubtfully referred to this species as, though it has the same colour pattern, it is even more obese, is smaller, with one whorl less, and the gemmules are even relatively larger. Further material may necessitate its separation either as a species or race.

Opimaphora litorea, sp. nov.

Figs. 162–165

Shell small, medially inflated, restricted at the base, summit narrow and elongate, colour deep red-brown, protoconch paler. Protoconch conical, of 5 whorls, the nucleus small and domed, other whorls with a single sharp keel overridden by fine axial threads. Mature whorls 7, sutures not well defined. Sculpture of 2 equal rows of rather small, rounded gemmules, 16 to the whorl, nearly their own diameter apart, rising above narrow spiral keels, and connected axially by narrow ribs. A third small median row develops on the last 3 whorls, the body whorl has an extra, nearly smooth spiral keel anteriorly, and there are 2 small, thin, smooth spiral keels on the rounded base. Aperture rounded to polygonal, expanded, the anterior spur on the type not

reaching the columella, though on older specimens it does so, posterior canal a rounded sinus. Columella column short, slightly oblique, broad, rounded anteriorly. Length 3·8 mm.

Localities.—Bowen, under rocks (J. Laseron), holotype (Figs. 162 and 163) and six paratypes; Darwin (J. Laseron) (Figs. 164 and 165).

Remarks.—This is the first of several species showing the progressive development of the small median row of gemmules between the two main rows. The deep colour is a good guide to recognition. The form varies somewhat, and some specimens are more inflated and other less inflated than the type. The Darwin specimens, one of which is figured (Figs. 164 and 165), are much lighter in colour than those from the type locality, and the gemmules are slightly larger, but they are otherwise indistinguishable.

Opimaphora integra, sp. nov.

Figs. 166 and 167

Shell small, but large for the genus, apex acuminate, spire medially inflated, restricted at the base, colour of protoconch and columella yellowish, remainder pure white. Protoconch small, slender, and conical, of 6 whorls, nucleus small, other whorls with a single sharp spiral keel overridden by fine axial threads, mature sculpture beginning abruptly. Mature whorls 8, sutures well defined. Sculpture on the early whorls 2 equal rows of gemmules, with a third small median row developing halfway down the spire, the body whorl with 3 rows, the upper the largest, and anteriorly an extra partly tuberculate spiral keel, with another smooth spiral keel on the rather flat base. The gemmules are large, rounded, 20 to the whorl, less than half their diameter apart, rising from low, broad spiral keels, axial connections not distinct. Aperture rounded and expanded, the anterior spur sharply bent, but not reaching the columella, posterior canal a shallow sinus, but the type may not have reached full development. Columella column short, narrow, rounded anteriorly. Length 4·8 mm.

Locality.—Murray Island (C. Hedley), holotype.

Remarks.—This is rather larger than other species of the genus, and the pure white colour should facilitate recognition. As with one or two other species the aperture has not attained full development of the twofold type, but limited material has made it impossible to determine if this is due to the stage of maturity. If further material proves that such species as *integra* never advance beyond the simple type of aperture, it will be necessary to separate them from *Opimaphora* as a new genus.

Opimaphora metellona, sp. nov.

Figs. 168 and 169

Shell small, inflated, the lower portion of the spire nearly cylindrical and only slightly restricted at the base, the apex slender, the first 3 mature whorls white, the protoconch and remainder pale yellow, in the paratype with a pinkish tinge. Protoconch relatively large, conical, of 5 whorls, the nucleus and first whorl smooth, the others with a single spiral keel and faint axial threads. Mature whorls 7, sutures

distinct. Sculpture 2 equal rows of gemmules with a third small median row developing on the lower portion of the spire, the body whorl with an additional small row anteriorly and two small smooth spiral keels on the base. The gemmules are rounded, of moderate size, 20 to the whorl, close together, rising above well-defined spiral keels, and connected axially by well-defined ribs. Aperture in the type may not be fully developed, the outer margin is flattened, the anterior spur not quite reaching the columella (though it does in the paratype), the posterior canal a shallow sinus. Columella column nearly straight, rounded anteriorly, ridged on the inner margin. Length 3·2 mm.

Locality.—Barrier Reef off Cairns (D. Pitt), C.46007 in Australian Museum, holotype and one paratype.

Remarks.—This species resembles *O. litorea* in form, but apart from the colour has the sutures more defined and a larger protoconch, though with one whorl less. The paratype is slightly narrower than the holotype, but otherwise conforms in all characters.

Remarks.—Closely related species are those next described, *A. islandica*, sp. nov., and *alveata*, sp. nov., both from the Barrier Reef. Summarizing the differences, *islandica* has smaller, more numerous and closely packed gemmules, and *alveata* is white with the upper row of gemmules smaller than the other rows.

Aclophora islandica, sp. nov.

Figs. 187–189

Shell of medium size, elongate, conical, the spire slightly convex, apex blunt, colour a uniform yellow-brown. Protoconch slightly worn in the type, but with a dome-shaped slightly tilted nucleus, the next whorl nearly smooth, the next with obscure spiral keels. Total whorls inclusive of the apical whorls 11, parted by deeply channelled sutures. Sculpture 3 equal rows of small, rounded gemmules, closely packed together, about 24 to the whorl, the rows close together and connected by narrow axial ribs, the body whorl with an additional partly tuberculate keel and a smooth spiral keel on the rounded base. Aperture of simple type, possibly not fully mature, the anterior spur slight and not reaching the columella, posterior canal also not fully developed, probably shallow. Columella column straight, short, broad, crossed by a rounded fold, rounded anteriorly. Length 6 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype (Fig. 187) and one paratype; Heron Island; 17–20 fm Masthead Island (C. Hedley) (Figs. 188 and 189).

Remarks.—*A. islandica* can be readily separated from *A. kerslakei* by the much smaller, closely packed gemmules. The two specimens from Masthead Island do not quite conform to the type, as they are smaller and the gemmules are not quite so closely packed. One, 3·8 mm long, is here figured for comparison (Figs. 188 and 189), but more material is needed to decide any limit of variation and whether geographical races have developed in any one area.

Aclophora alveata, sp. nov.

Fig. 190

Shell of medium size, conical with convex sides, slightly restricted at the base, the penultimate whorl larger than the body whorl, the holotype uniformly white, the paratype with a purplish tinge. Protoconch cylindrical, the nucleus dome-shaped and tilted, the next 2 whorls nearly smooth, the third with a faint spiral keel. Remaining whorls 8, slightly rounded, parted by deep channelled sutures. Sculpture throughout of 3 rows of gemmules, the upper row the smallest, the other 2 nearly equal, the gemmules moderately large, rounded, 16–18 to the whorl, about half their diameter apart, rising above well-defined spiral keels, axial connections not well developed. On the body whorl the 3 rows are practically equal though smaller, and there is an additional partly tuberculate keel and a smooth spiral keel on the rounded base. Aperture of simple type, the anterior spur sharply bent, but not reaching the columella, posterior canal a shallow sinus. Columella column short, broad, slightly oblique, a broad fold near its base, rounded anteriorly. Length 5·5 mm.

Localities.—Michaelmas Cay (T. Iredale), holotype and one paratype; 4–14 fm Albany Passage (C. Hedley).

Remarks.—Closely related to both *A. kerslakei* and *A. islandica*, but differing from both in colour and form, by the rounded whorls, and by having the upper row of gemmules smaller than the others. A long series from Albany Passage correspond closely to the type, except that they are less restricted at the base, and they also vary in size, some specimens being appreciably smaller.

Aclophora albozonata, sp. nov.

Figs. 191 and 192

Shell small, conical with slightly convex sides, and slightly restricted at the base, colour white, with bands of yellow-brown covering the upper row of gemmules and the sutures, base yellow-brown. Protoconch cylindrical, the nucleus small and tilted, the next 3 whorls nearly smooth, faint spiral keels gradually developing and breaking into gemmules. Remaining whorls 7, separated by deep channelled sutures. Sculpture on the first mature whorl 2, on the remainder 3 equal rows of moderately large rounded gemmules, 16 to the whorl, about half their diameter apart, rising above defined spiral keels, and connected axially by short narrow ribs. The body whorl has an extra partly tuberculate keel and another smooth spiral keel on the base. Aperture rounded, anterior spur not reaching the columella, the anterior canal quite open, posterior canal a shallow sinus. Columella column nearly straight, with a thick callus on the inner margin. Length 3·6 mm.

Locality.—Darwin (J. Laseron), holotype and three paratypes.

Remarks.—This species is readily separated from all other species of *Aclophora* by its colour pattern, though in this character it resembles *Coriophora tigris*, previously described. *C. tigris* has, however, quite different sculpture, and by this and the aperture is placed in another genus.

Genus TETRAPHORA, gen. nov.

Type species *Tetraphora mapoonensis*, sp. nov.

Tetraphora is proposed for shells which resemble *Notosinister* in form, in the simple aperture, and in the deeply channelled sutures, but differ by having 4 rows of gemmules instead of 3. The protoconch of the type species is unknown, but in the second species assigned to the genus, *T. borealis*, sp. nov., the protoconch is slender, multi-whorled, with a single sharp spiral keel crossed by axial threads.

Tetraphora mapoonensis, sp. nov.

Fig. 193

Shell of medium size, conical, spire very slightly convex, not restricted at the base, colour uniform cream. Protoconch unknown. Remaining whorls 11, of which the upper 2 may be the basal whorls of the protoconch, sutures deeply channelled. Sculpture 4 equal rows of small gemmules throughout the spire, the rows close together, the gemmules 18 to the whorl, close together, rising above defined spiral keels and axially connected by short ribs, the body whorl with 3 additional spiral keels on the base, the upper partly tuberculate. Aperture not quite fully developed in the type, the outer margin straight, the anterior spur only partially developed and not reaching the columella, the posterior canal not apparent. Columella column straight, tapering anteriorly, with a heavy plate of callus on the inner margin. Length 5·8 mm.

Locality.—Mapoon, Gulf of Carpentaria (C. Hedley), C.14296 in Australian Museum, holotype and one paratype.

Remarks.—It is unfortunate that more and better material is not available for the description of this, the type of its genus, but the general characters are sufficiently distinctive, particularly the four rows of gemmules, and there should be no difficulty in its future recognition both specifically and generically.

Tetraphora borealis, sp. nov.

Figs. 194 and 195

Shell of medium size, conical, elongate, acuminate, with nearly straight sides, colour white. Protoconch conical in the line of the spire, acuminate, of 5 whorls with a single sharp spiral keel overridden by strong axial threads, the first mature whorl overlapping the last whorl of the protoconch. Mature whorls 12, sutures narrow and deeply channelled. Sculpture 3 rows of gemmules on the earlier whorls, 4 on the last 4 whorls, thus bringing the species within *Tetraphora*. The fourth row is at first small between the first and second posterior rows, becoming larger and of equal value on the body whorl. The body whorl has another additional row anteriorly and a smooth spiral keel on the flattened base. The gemmules are small, 18 to the whorl, about their own diameter apart, rising from well-defined narrow spiral keels, and connected axially by raised ribs, leaving deep pits in the interstices. Aperture in the type probably not fully matured, the anterior spur and posterior canal not yet developed, but apparently of the simple type. The columella column is not oblique,

but is slightly bent and narrowed anteriorly, with a heavy plate of callus on the inner margin. Length 7·5 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype.

Remarks.—The four rows of gemmules on the later whorls bring this species within *Tetraphora* and distinguish it from any species of *Notosinister* which it might otherwise resemble. Compared with *T. mapoonensis* it is larger, slenderer, with more whorls, the spire is straighter, and the fourth row of gemmules is absent on the earlier whorls.

Opimaphora impara, sp. nov.

Figs. 170 and 171

Shell small, medially inflated, restricted anteriorly, apex slender and cylindrical, protoconch and first 2 mature whorls white, remainder yellow with the upper row of gemmules white. Protoconch cylindrical, narrow, of 4 whorls, the nucleus dome-shaped, other whorls with faint spiral keels and faint axial threads on the base. Mature whorls 7, sutures distinct. Sculpture on the early whorls 2 equal rows of gemmules, on the later whorls 3, the upper much the larger, with the gemmules oval and elongated axially, very close together, 16 to the whorl, the median row small, the lower row intermediate in size, neither spiral nor axial connections distinct. The body whorl still has the upper row largest, while below this are 3 small equal rows, with a single smooth spiral keel on the base. Aperture polygonal, thin, expanded, the anterior spur not quite reaching the columella, but probably not at its fullest development, posterior canal a shallow sinus. Columella column short, crossed by a broad fold, nearly straight, rounded, and ridged anteriorly. Length 3·8 mm.

Locality.—5–8 fm Murray Island (C. Hedley), holotype.

Remarks.—The large, oval, closely packed gemmules of the upper row, and the inequality of the different rows are so distinctive that, though this species is based on a single specimen, there should be no difficulty in its future recognition.

Opimaphora trichroma, sp. nov.

Figs. 172 and 173

Shell small, bottle-shaped, medially swollen, restricted at the base, protoconch yellow, the next 2 whorls white, the next deep chocolate, remainder and base yellow. Protoconch of 5 short whorls, the nucleus tilted, the remainder with 2 faint spiral keels without axial threads. Mature whorls 6, sutures only distinguishable by the difference in colour of the whorls. Sculpture 2 rows of gemmules, with a third small median row on the penultimate whorl, the body whorl with 3 equal rows and a smaller row on the rounded base. The gemmules are large, round, 14 to the whorl, closely packed, spiral and axial connections not distinguishable. Aperture small, quadrangular, outer margin straight, the anterior spur sharply bent but not reaching the columella, anterior canal a shallow rounded sinus. Columella column short, nearly straight, broad, anteriorly truncate, a narrow callus on the inner margin. Length 2·8 mm.

Locality.—Michaelmas Cay (T. Iredale), holotype.

Remarks.—The striking variegated colouration with the strong chocolate band in the centre should facilitate the future recognition of this species. Other distinguishing features are the relatively few large gemmules and the protoconch.

Opimaphora molecula, sp. nov.

Figs. 174 and 175

Shell minute, bottle-shaped, spire convex, slightly restricted at the base, apex subulate. Protoconch subulate, relatively large, with a slight taper, of 5 whorls, appearing smooth under ordinary magnification; but with a magnification of 40 diameters 2 faint spiral keels and axial threads are visible. Mature whorls 4, slightly rounded and restricted at the sutures. Sculpture of 3 rows of gemmules, the lower 2 equal, the upper smaller, except on the body whorl, where all three are equal, with a smaller anterior row and 2 small smooth spiral keels on the base. The gemmules are rounded, close together both spirally and axially, 18 to the whorl, without apparent axial or spiral connections. Aperture simple and not expanded, subquadrangular, the anterior spur not reaching the columella, the posterior canal a shallow sinus. Columella column short, straight, with an oblique anterior margin. Length 2 mm.

Locality.—15 fm Cambridge Gulf, north-west Australia (G. Whitley), holotype.

Remarks.—There is no other species with which this can readily be compared. The minute size, form, subulate protoconch, deep sutures, and three rows of gemmules are all distinctive characters.

Genus ACLOPHORA, gen. nov.

Type species *Aclophora robusta*, sp. nov.

Medium to large robust shells with from 9 to 12 mature whorls, the sutures deeply channelled and often threaded, protoconchs short and obtuse, sculpture of 3 rows of gemmules throughout, which are medium to small in size, and connected both spirally and axially. When the gemmules are small and distant the sculpture tends to become cancellate. Aperture of simple type, not becoming tubular after maturity.

This seems a natural group close to *Notosinister* Finlay, but distinguished by the larger shells and more particularly by the protoconch. Among southern Triphoridae such species as *cinerea* Hedley may be transferred from *Notosinister* to *Aclophora*.

Aclophora robusta, sp. nov.

Fig. 176

Shell of medium size, broadly conical with slightly convex sides, colour variegated, mainly red-brown, the type with a white apex and occasional rows of white gemmules, other specimens with a dark apex and the white rows of gemmules irregularly dispersed. Full protoconch unknown, but apparently of 2 whorls, the second with a single spiral keel and faint axial threads. Mature whorls 9, short, the sutures very deeply channelled and bearing a spiral thread. Sculpture throughout

of 3 rows of smooth rounded gemmules, of moderate size, varying in number, 22 to the whorl on the type, but other specimens generally with about 20, the gemmules close together and connected both spirally and axially by smooth rounded bars, the interstices deep pits. An extra row of gemmules is on the body whorl, and a single, nearly smooth spiral keel below this on the base. Aperture rounded, of simple type, the anterior spur not reaching the columella but bent back anteriorly to border a rather long anterior canal, anal notch shallow. Columella pillar short, slightly oblique, rounded anteriorly, a heavy callus on its inner margin. Length 8·5 mm.

Localities.—Curtis Island (J. Laseron), holotype and one paratype; Lady Elliot Island (C. Hedley), C.8786 in Australian Museum; Caloundra (common); Hayes Island, Moreton Bay (G. Gross), common, C.49201.

Remarks..—This is a common and widespread species in southern Queensland, but has so far not been seen north of Port Curtis. Though the species is common it has been difficult to obtain good material, but even fragments are easy to recognize by their robust form, sculpture, and variegated brown and white colouration.

Aclophora grandiosa (Laseron)

Fig. 177

Notosinister grandiosa Laseron, 1954, p. 155, fig. 30.

The species was named from a single imperfect specimen from Woolgoolga in northern New South Wales, and it was then stated that its large size and distinctive characters should make its future recognition easy. It was also anticipated that its main habitat would be Solanderian. Another single and also imperfect specimen from Caloundra adds to this probability. There was no difficulty in its recognition and it conforms in every particular to the holotype. The specimen is here figured, and its length is 13 mm, practically the same as the type. Good recognition points are the size, deeply channelled sutures, numerous small gemmules, 24 or more to the whorl, and the strong spiral and axial connections. The aperture is peculiar as seen by the figure, but whether this is due to immaturity or a malformation is impossible to determine without more material.

Aclophora sp.

Fig. 178

A single specimen of what is probably a different species was collected by J. Laseron at Darwin, and is here figured for future reference. Its length is 7·7 mm. Unfortunately it is not quite mature and the outer margin of the aperture is broken, so that it is impossible to give a description full enough for definite specific determination. The colour is a uniform cream, there are 9 mature whorls, and 2 whorls left of a columnar protoconch, which was too worn to ascertain details. The sutures are deeply channelled and bear a smooth spiral thread. The gemmules are small, in 3 equal rows, about 22 to the whorl, ill defined, rising above broad spiral keels, and connected axially by strong ribs. Aperture not fully developed, but probably of the simple type.

Aclophora tropica, sp. nov.

Fig. 179

Shell of medium size, regularly conical with straight sides, colour creamy yellow with irregular splashes of yellow-brown, the base yellow-brown. Protoconch short, in the type worn, but apparently with a dome-shaped nucleus with incipient sculpture on the next whorl. Remaining whorls 8, separated by deep channelled sutures. Sculpture throughout of 3 equal rows of large rounded gemmules, 20 to the whorl, about half their diameter apart, rising above low broad spiral keels, and connected axially by narrow bars. Body whorl with 4 rows of gemmules and an excavate base. Aperture rounded, simple, the anterior spur not reaching the columella, leaving the anterior canal quite open, but the type has apparently just reached maturity, and this character might be slightly modified with age. Posterior canal a rounded sinus. Columella column long and nearly straight, rounded anteriorly, the inner margin with a heavy plate of callus. Length 5·5 mm, width 1·8 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and two paratypes.

Remarks.—This is a typical *Aclophora*, but readily distinguishable from the southern Queensland specimens by the colour pattern, the straight-sided spire, and details of the sculpture and aperture.

Aclophora linearis, sp. nov.

Figs. 180 and 181

Shell large, elongated, conical, acuminate, spire with nearly straight sides, colour a uniform cream. Protoconch very small, planoidly coiled on the summit. Mature whorls 16, sutures deeply channelled. Sculpture throughout of 3 equal rows of small gemmules, 18 to the whorl, about their own diameter apart, rising above well-defined, elevated, narrow, rounded spiral keels, and connected axially by raised narrow ribs, leaving the interstices as deep pits, the body whorl with an extra anterior row of gemmules, and a smooth spiral keel on the flattened base. Aperture rounded, expanded, the outer and anterior margins reflected, the anterior spur reaching the columella and very sharply bent, the anterior canal open, the posterior canal a deep narrow V-shaped sinus. Columella column nearly straight, tapering and acute anteriorly, a heavy callus on the inner margin. Length 10·8 mm.

Locality.—20 fm Lindeman Island (T. Iredale), holotype.

Remarks.—The long, straight, slender spire separates this from all the other species here described. The protoconch is also distinctive.

Aclophora conferta, sp. nov.

Fig. 182

Shell of medium size, elongated, lower portion of spire cylindrical, conical towards the apex, colour a uniform pale yellow. Protoconch unknown. Whorls at least 13, flattened, separated by deep narrow sutures. Sculpture throughout of 3 equal broad spiral keels, very close together, broken into flattened, almost square

gemmules, packed closely together, about 26 to the whorl, and connected axially by short, broad ribs. The body whorl has 2 extra keels on the rounded base, the anterior one nearly smooth. Aperture large, rounded, and expanded, of simple type, the anterior spur sharply bent and reaching the columella, posterior canal broken away in type. Columella column short and broad, slightly oblique, narrowed anteriorly, and crossed by a prominent fold. Length 8·5 mm.

Localities.—Angowrie, near Clarence River, New South Wales (A. A. Cameron), holotype; Caloundra (Mrs. J. Kerslake).

Remarks.—The closely packed, irregular gemmules give this species a distinctive facies, and in this it resembles *Coriophora capricornia*, from which, however, it is readily separated both generically and specifically by the form, deep sutures, and the three rows of gemmules right up the spire. Like *Nanaphora tricolor* and *Aclophora grandiosa*, though the holotype comes from a Peronian locality, it is apparently a tropical form with its main habitat in southern Queensland.

Aclophora axialis, sp. nov.

Figs. 183 and 184

Shell of medium size, elongate, conical, the spire with straight sides, apex blunt, colour white. Protoconch of 3 whorls, the nucleus large and slightly tilted, the other 2 somewhat inflated with a single blunt spiral keel, axial sculpture not detected. Mature whorls 10, sutures narrow and deeply channelled. Sculpture throughout 3 spiral keels, 4 on the body whorl, the keels surmounted by small ill-defined gemmules, about 26 to the whorl, and connected axially by strong cords, which are continuous below the lower row to the sutures. A smooth spiral keel is additional on the flattened base. Aperture rectangular, the outer margin straight and continuous with the line of the spire, the anterior spur not reaching the columella, posterior canal a U-shaped sinus. Columella column straight, pointed anteriorly. Length 6·4 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype.

Remarks.—The well-defined spiral keels with the ill-defined small gemmules and strong axial cords give the sculpture a cancellate appearance, which should make its future recognition easy.

Aclophora cancellata, sp. nov.

Fig. 185

Shell large, elongate, conical, the spire with straight sides, colour white. Protoconch unknown. Mature whorls 16, sutures narrow and deep, each marked by a thin spiral cord. Sculpture throughout of 3 narrow elevated spiral keels, 4 on the body whorl, which rise above and override well-defined narrow axial ribs, producing ill-defined gemmules more than their own diameter apart, 16 to the whorl, the whole sculpture strongly cancellate. Base flattened. Aperture probably not quite mature, rounded, the anterior spur and posterior canal not yet developed. Columella column straight and tapering anteriorly. Length 11·5 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and one paratype.

Remarks.—Though the full characters of the protoconch and aperture are unknown, the sculpture is that of a typical *Aclophora*, and the wide cancellation should facilitate its future recognition. Its nearest relative is probably *cinerea* Hedley from the Peronian Province.

Aclophora kerslakei, sp. nov.

Fig. 186

Shell of medium size, stout, conical with a slightly convex spire, colour a uniform yellow-brown. Protoconch large, cylindrical, a small tilted nucleus, followed by a slightly inflated smooth whorl with a vitreous texture, the next 2 whorls with first 1 and then 2 faint spiral keels which gradually break into gemmules. Remaining whorls 8, parted by deep sutures. Sculpture throughout of 3 equal rows, close together, of medium-sized, rounded gemmules, 18 to the whorl, rising from narrow keels, about half their diameter apart, and connected axially by short, broad ribs, the body whorl with 2 additional nearly smooth spiral keels on the rounded base. Aperture simple, not extended, the outer margin nearly straight, the anterior spur not reaching the columella, posterior canal not determinable as the outer margin of the holotype is slightly broken. Columella column short, straight, swollen at the base, tapering and rounded anteriorly, a heavy callus on the inner margin. Length 6·5 mm.

Locality.—Peel Island, Moreton Bay (Mrs. J. Kerslake), holotype and four paratypes selected from a number of specimens.

Genus NOTOSINISTER Finlay

Notosinister Finlay, 1927, p. 384.

Type species *Triphora fascelina* Sutor.

The type is a New Zealand species, and Finlay based his genus purely on the protoconch, which is described as of 4 whorls, the first smooth, the others spirally keeled with axial threads between. This by itself is insufficient, for this type of protoconch, with a varying number of whorls, appears in many otherwise dissimilar groups right through the family. At that time the importance of the protoconch was being increasingly recognized, and rather unfortunately Finlay, as well as some other conchologists, hailed it as the answer to all phylogenetic problems. This has brought many otherwise incongruous species together, and has caused some confusion.

In Australia *Notosinister granifera* (Brazier), a Peronian species, is very close to the type species, and can be considered typical of a large group with a wide range, comprising many southern Australian species, and spreading into the tropics to as yet an unknown extent, but certainly as far as Darwin.

The protoconch is as Finlay states, and it can be taken as one only of the characteristics of the genus. Other definite characters are that the shells are nearly all small, generally ranging from 4–8 mm in length, they are slender, the spires with flat sides, the sutures are deep and channelled, the sculpture consists of 3 rows

of gemmules, and the aperture is of the simplest type, the posterior canal a shallow sinus or notch, the anterior margin bent into a spur which often does not reach the columella.

The colour varies with the species, but is often a uniform brown.

Within this definition are many tropical species which are here assigned with some confidence to *Notosinister*, but there are some with rather a different facies, and further research may necessitate a subdivision.

Notosinister rufula (Watson)

Figs. 196 and 197

Triforis rufula Watson, 1886, p. 566, pl. 42, fig. 2.

The type locality is 8 fm off Wednesday Island, Torres Strait. It is a well-defined small, rather stout species, with a uniform greyish yellow colour, a 4-whorled protoconch with a double spiral keel crossed by axial threads, deeply channelled sutures, 3 rows of gemmules, and a simple aperture, the anterior spur not reaching the columella. It is thus a typical *Notosinister*.

The species evidently has a wide range. The specimen figured is from 20 fm off Endeavour Reef (D. Pitt), and is 4 mm long. Other specimens examined are from 15–20 fm off Point Charles, Darwin (M. Ward), a long way to the west, and from 17–20 fm off Masthead Island (C. Hedley), C.21615 in Australian Museum, well to the south. It has also been noted in many intermediate localities. Beyond a little difference in width, specimens from all localities match each other and Watson's description and figure.

Notosinister stipara, sp. nov.

Figs. 198 and 199

Shell of medium size, stout, conical, spire slightly convex, colour a uniform cream. Protoconch conical, acuminate, of 5 whorls, the nucleus small and domed, remainder with a prominent, sharp, single spiral keel, crossed by faint axial threads. Mature whorls 9, separated by deeply channelled sutures. Sculpture throughout 3 equal, nearly touching rows of gemmules, 4 rows on the body whorl, the gemmules closely packed, 22 to the whorl, irregular in shape, sometimes nearly square, base rounded, with an extra smooth spiral keel. Aperture large, polygonal, expanded, the anterior spur not reaching the columella, the posterior canal a U-shaped sinus. Columella column narrow, bent, and slightly oblique, rounded anteriorly. Length 6·2 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and one paratype.

Remarks.—This species can readily be distinguished among other species of *Notosinister* by the closely packed irregular gemmules. In this character it resembles, however, both *Mesophora pavimenta* and *Coriophora capricornia*, previously described, but the three rows of gemmules and the deep sutures at once separate it.

Notosinister micans, sp. nov.

Figs. 200 and 201

Shell very small, medially inflated, restricted at the base, colour a deep red-brown, almost black. Protoconch conical, of 4 whorls, the nucleus relatively broad and dome-shaped, the other whorls with a single spiral keel crossed by axial threads. Mature whorls 6, the sutures deep and narrow. Sculpture throughout of 3 rows of small round gemmules, 18 to the whorl, slightly more than their own diameter apart, rising above well-defined spiral keels, and connected axially by narrow ribs. On the body whorl there are 4 rows of gemmules, but on the lower 3 rows the gemmules become ill-defined, the sculpture becoming markedly cancellate, and there are 2 additional, smooth spiral keels on the rounded base. Aperture relatively large, the outer margin rounded and reflected, the anterior spur not reaching the columella, posterior canal a barely discernible shallow sinus. Columella column short, slightly oblique, rounded anteriorly, ridged on its inner margin. Length 2·8 mm.

Locality.—Under rocks, Bowen (J. Laseron), holotype and three paratypes.

Remarks.—Compared with *N. rufula* (Watson), with which it seems closely related, it is smaller, more inflated, and has a single instead of a double keel on the protoconch. Actually it is more easily confused with *Opimaphora litorea*, previously described, with which it is associated. Both are small, though *micans* is the smaller; they have the same colour and appearance, but the deep sutures and three rows of gemmules place *micans* in a different group.

Notosinister stricta, sp. nov.

Figs. 202 and 203

Shell of medium size, conical, spire slightly convex, colour a bright golden yellow. Protoconch conical, of 5 whorls, the first 2 nearly smooth, the last 2 with 2 sharp spiral keels crossed by fine axial threads. Mature whorls 9, slightly rounded, sutures deeply channelled. Sculpture of 3 almost touching rows of gemmules, the uppermost slightly smaller than the others, the gemmules 19–20 to the whorl, closely packed, rather irregular in form but mostly circular. There are 4 rows of gemmules on the body whorl, and a nearly smooth spiral keel on the base. Aperture expanded, polygonal, the anterior spur not reaching the columella, posterior canal a U-shaped sinus. Columella column nearly straight, tapering anteriorly, inner margin with a narrow ridge. Length 6·3 mm.

Locality.—Mornington Island (C. Hedley), C.14606 in Australian Museum, holotype.

Remarks.—The golden colour and slightly rounded whorls are good recognition points for this species. It resembles *N. stipata* in the close packing of the gemmules, but it is narrower, the gemmules are fewer, and the protoconch has a double instead of a single spiral keel.

Notosinister subaura, sp. nov.

Figs. 204 and 205

Shell of medium size, elongate, lower portion of spire cylindrical, upper portion conical, colour a uniform golden brown. Protoconch of 4 whorls, the nucleus tilted,

the last 2 whorls with 2 spiral keels crossed by fine axial threads. Mature whorls 12, sutures deeply channelled. Sculpture throughout of 3 rows of gemmules, the middle row slightly larger than the others, the gemmules small, rounded, 20 to the whorl, about their own diameter apart, rising above well-defined spiral keels, and connected axially by narrow ribs. The body whorl has 4 rows of gemmules, and a smooth spiral keel on the flattened base. Aperture rounded, not expanded, the anterior spur reaching the columella and sharply folded, posterior canal a U-shaped sinus. Columella column narrow, bent, and oblique, crossed by several narrow cords, inner margin with a thick, wide, almost detached callus. Length 7 mm.

Locality.—Murray Island (C. Hedley), C.29997 in Australian Museum, holotype.

Remarks.—Though again described from a single specimen, this is a distinctive species, separable from the preceding species by the elongate form, more numerous whorls, smaller and more widely separated gemmules, and to a lesser extent by the aperture.

Notosinister subulata, sp. nov.

Figs. 206 and 207

Shell small, slender, conical, acuminate, spire with flat sides, colour of type cream (may be faded), other specimens ranging to a uniform yellow-brown. Protoconch conical, long and slender, of 7 whorls, the last 4 with 2 sharp spiral keels crossed by fine axial threads. Mature whorls 8, separated by deep channelled sutures. Sculpture throughout of 3 equal rows of small gemmules, the rows close together, the gemmules rounded, 18 to the whorl, about half their diameter apart, alternating on adjacent rows, rising above distinct spiral keels, and connected axially by narrow ribs. The body whorl has 4 rows of gemmules and a smooth spiral keel on the base. Aperture polygonal, expanded, the margin reflected, the anterior spur sharply bent and not reaching the columella, the posterior canal a very deep, rounded sinus. Columella column slightly oblique, rounded anteriorly, a layer of callus on the inner margin. Length 4·6 mm.

Locality.—20 fm off Endeavour Reef (A. McCulloch), holotype and five paratypes.

Remarks.—The slender, straight-sided conical spire, and the long slender protoconch are useful recognition points for this species, and it also differs from others in details of the sculpture and aperture.

Notosinister hopensis, sp. nov.

Figs. 208 and 209

Shell of medium size, elongate, conical, spire with nearly straight sides, colour uniformly yellow, the base yellow-brown. Protoconch conical, of 4 whorls, the first nearly smooth, remainder with 2 spiral keels crossed by fine axial threads. Mature whorls 10, separated by deep channelled sutures. Sculpture throughout of 3 equal rows of gemmules, the rows nearly touching, the gemmules rounded, 14–15 to the whorl, about their own diameter apart, rising above well-defined spiral keels, body whorl with a fourth partially tuberculate spiral keel and another smooth spiral keel on the flattened base. Aperture rounded, expanded, the anterior spur reaching the

columella, posterior canal a shallow rounded sinus. Columella column short, oblique, rounded anteriorly. Length 5 mm.

Localities.—5–10 fm off Hope Islands (C. Hedley), holotype; 20 fm off Endeavour Reef (A. McCulloch).

Remarks.—This species is close to the preceding species *N. subulata*, but is not quite so slender, the gemmules are fewer and farther apart, and more particularly the protoconch is less slender and has two fewer whorls.

Notosinister diminuta, sp. nov.

Figs. 210 and 211

Shell very small, relatively broad, acuminate, somewhat swollen medially and restricted at the base, colour a uniform brown. Protoconch relatively large, acuminate, of 6 whorls, with a single sharp spiral keel, overridden by strong axial threads. Mature whorls 5, separated by deep channelled sutures. Sculpture throughout of 3 equal rows of gemmules, the rows close together and almost touching, the gemmules large, 18 to the whorl, close together and almost touching, the body whorl with a fourth row of gemmules and 2 smooth spiral keels on the rounded base. Aperture relatively large, outer margin nearly straight and reflected, the anterior spur sharply bent and not reaching the columella, posterior canal a rounded sinus. Columella column short, nearly straight, and rounded anteriorly, a thick callus on the inner margin. Length 2·5 mm.

Localities.—Darwin (J. Laseron), holotype; 15–20 fm off Point Charles, Darwin (M. Ward); Cambridge Gulf, north-west Australia (G. Whitley).

Remarks.—This is nearly the smallest of all the Triphoridae here described. In colour and form it resembles *N. micans* from Bowen, but is narrower, has larger and closer gemmules, and the protoconch is relatively much larger and has six instead of four whorls.

Notosinister constricta, sp. nov.

Figs. 212 and 213

Shell of medium size, lower portion of spire nearly cylindrical, upper portion conical, elongate, acuminate, colour uniformly white. Protoconch of 5 whorls, conical, acuminate, nucleus small, other whorls with a single, sharp spiral keel overridden by fine axial threads, the protoconch terminated and divided from mature sculpture by a diagonal line. Mature whorls 8, rounded, restricted at the deep sutures which are occupied by a smooth spiral thread. Sculpture throughout of 3 equal rows of rounded gemmules, 18 to the whorl, close together and connected axially by narrow ribs. The body whorl has 4 rows of gemmules and a smooth spiral keel on the flattened base. The aperture is probably not fully developed as the posterior canal is not apparent, but it is nearly square, the anterior spur not reaching the columella. Columella column slightly oblique and rounded anteriorly. Length 5·5 mm.

Locality.—15–20 fm off Point Charles, Darwin (M. Ward), holotype and two paratypes.

Remarks.—The rounded whorls restricted at the sutures which carry a spiral thread distinguish this from all other species here described. In form it is nearest to *N. subaura*, but has different sculpture and a different protoconch.

VI. Description of Species from Christmas Island

Christmas Island is a small isolated oceanic island rising from great depths in the Indian Ocean south of Java at lat. 10° S. and long. 105°42′ E., about 600 miles north-west of the nearest Australian coast, and well beyond the physical boundaries of the Timor Sea. It has a large and varied molluscan fauna, most of which has not yet been identified, and thus its geographical correlation is unknown, though probably many of the species will be found to be endemic. The species here described came from a small dredging from 100 fm on the steep slopes on the island, and most are probably shallow-water forms which have rolled or been washed down. From this material T. Iredale has already described several peculiar and apparently unique genera of small gasteropods, and the author has described another unique gasteropod of the family Rissoinidae, and some Cerithiopsidae. Now from the same source 14 species of Triphoridae have been sorted, all of which are undescribed, including two new generic types. In addition were several species, the material of which was too imperfect for identification. The significance of this rich fauna in the distribution of the marine life of the Indian Ocean, and any possible relationship to Australian faunas is not yet understood.

Genus INIFORIS Jousseaume

Iniforis ordinata, sp. nov.

Figs. 214–216

Shell small, elongate, regularly conical, spire with nearly straight sides, acuminate, protoconch yellow-brown, remainder white. Protoconch conical, in line with the spire, acuminate, of 6 whorls, nucleus small and domed, remaining whorls with a single blunt keel crossed by axial threads, mature sculpture beginning abruptly. Mature whorls 11, short, sutures defined but not deep. Sculpture of 2 rows of large rounded gemmules rising from defined spiral keels, the lower row slightly larger, the rows close together without defined axial connections, the gemmules about half their diameter apart, 12–13 to the whorl, the body whorl with an extra anterior row. Aperture of well-developed threefold type, the true aperture tubular, elongated, and round, anterior canal elongated, tubular, tapering, anteriorly truncate, oblique, crossed by strong ribs near the base, posterior canal also tubular, long, and narrow. Length 4·6 mm. Holotype and five paratypes.

Remarks.—The nearest relative of this species is probably *Triphoris reevei* Deshayes (1867, p. 101, pl. 38) from Réunion, which has much the same form, colour, and sculpture, but *reevei* is described as having a mucronate apex, and the tubular extensions of the true aperture, and the anterior and posterior canals are not nearly so great.

Iniforis tuberia, sp. nov.

Figs. 217–219

Shell small, anteriorly inflated with convex sides, tapering towards the summit which is acuminate, colour yellowish white. Protoconch slender and acuminate, of 6 whorls, the nucleus small and flattened, remaining whorls with a single spiral keel crossed by spiral threads. Mature whorls 8, sutures distinct but shallow. Sculpture of 2 rows of very large, rounded gemmules, close together, rising from distinct spiral keels, the rows close together, an additional small row on the base of the body whorl. Aperture of the threefold type, the true aperture tubular and extended, round, the margin slightly reflected, anterior canal tubular, broad, and oblique, crossed by 2 ribs at its base, posterior canal relatively short, tubular, and cylindrical. Length 3·3 mm. Holotype and seven paratypes.

Remarks.—This is the smallest and most inflated of any of the species, and the very large gemmules afford another good recognition point. The form is slightly variable, and some specimens are even more inflated than the type and others are narrower.

Genus EPIFORIS Laseron

Epiforis radix, sp. nov.

Figs. 220–222

Shell small, conical, elongate, relatively narrow with slightly convex sides, apex blunt, colour white. Protoconch short, nucleus small, laterally placed on the apex, the next 2 whorls short with a single spiral keel but no axial cords, the third whorl with 2 keels, gradually breaking into gemmules. Mature whorls about 10, sutures not distinct. Sculpture 2 equal rows of gemmules, the gemmules rounded, 14–15 to the whorl, about half their diameter apart, rising above defined spiral keels but with no visible axial connections, the body whorl with an extra anterior smaller row. Aperture of the threefold type, the true aperture round, tubular, but not greatly extended, the anterior canal very large, tubular, tapering, straight, and greatly extended in the axis of the spire, posterior canal tubular, but relatively short. Length 4·7 mm. Holotype and two paratypes.

Remarks.—Apart from the protoconch which distinguishes this species from all species of *Iniforis*, and brings it into *Epiforis* as proposed in the first part of this paper, the most striking character is the long straight anterior canal, and this should make its future recognition easy.

Epiforis decorata, sp. nov.

Figs. 223–225

Shell of medium size, conical, with slightly convex sides and a blunt apex, colour nearly white with a spiral band of yellow-brown crossing the lower row of gemmules. Protoconch short and broad, the nucleus large, domed, and tilted, the next whorl inflated with an obscure keel, the next short with a rounded spiral keel and incipient adult sculpture. Mature whorls 13, sutures distinct. Sculpture 2 equal rows of gemmules with a wavy spiral thread between, the gemmules rising from defined

keels, 14 to the whorl, about their own diameter apart, no axial connections visible, the body whorl with 3 smooth thin spiral keels on the base. Aperture of the threefold type, the true aperture tubular, round, extended with the margin slightly reflected, anterior canal tubular, long, and oblique, posterior canal tubular, narrow, and relatively very long. Length 6·1 mm. Holotype and eight paratypes.

Remarks.—The protoconch places this species within *Epiforis* and it differs from *E. radix* mainly by being broader and having a convex spire, and by the differences in the anterior and posterior canals. Both differ from *E. australis*, the type species, by having longer tubular extensions of the threefold aperture, and by the sculpture.

Genus CONTRAFORIS, gen. nov.

Type species *Contraforis insulana*, sp. nov.

Aperture of the threefold type, the true aperture, anterior and posterior canals all tubular and greatly extended, the shell narrow and attenuate, whorls relatively long, the sculpture of 2 widely separated rows of gemmules of which the upper is much the larger. Protoconch unknown.

The attenuate form, long whorls, and distinctive sculpture separate this genus from all others with the same type of aperture.

CONTRAFORIS INSULANA, sp. nov.

Fig. 226

Shell of medium size, elongate, narrow, and attenuate, the spire nearly cylindrical with very little taper, colour white. Protoconch unknown. In the holotype only 8 mature whorls remain, but judging from the angle of taper the full number is probably from 12–15. The whorls are long, the sutures distinct. Sculpture 2 unequal rows of gemmules, the upper much the larger, the gemmules wedge-shaped, 12 to the whorl, rising above well-defined spiral keels, axial connections absent, the body whorl with 2 extra small rows on the base. Aperture threefold, true aperture round, tubular but not greatly extended, anterior canal tubular, long, straight, in the line of the spire, encircled by a rounded rib, posterior canal tubular, relatively very long, swollen near the base. Length 6·6 mm. Holotype only.

Remarks.—Though only one specimen without the apical whorls is known, a new genus and species is proposed, as the characters are distinctive, and will not fit into any other known group with the threefold aperture.

Genus LINIPHORA, gen. nov.

Type species *Liniphora restis*, sp. nov.

Shells exceedingly narrow and attenuate, the spire cylindrical with only a slight taper in its upper portion, whorls long, sculpture 2 widely separated rows of gemmules, the lower the larger, protoconch multi-whorled, aperture simple.

This genus stands out from any other of the family by its extremely attenuate form, even more attenuate than such groups as *Inella*, *Viriola*, and *Subulophora*.

The long whorls and sculpture are also distinctive. *Triphora asperrimus* Hinds, described from New Guinea, may come here, but an immature specimen from Funafuti, tentatively identified by Hedley (1899, p. 559, fig. 77) as *asperrimus* shows a different type of sculpture and an aperture which suggests a different family altogether, though the shell is sinistral.

Liniphora restis, sp. nov.

Figs. 227 and 228

Shell of medium size, cylindrical, narrow, and exceedingly attenuate, white. Protoconch of holotype broken, but from another immature specimen it is slender, continuing the line of the spire, multi-whorled, with a double spiral keel and fine axial threads. Mature whorls of holotype 16, but judging from immature specimens probably 20 when complete, sutures not discernible, whorls long. Sculpture of 2 well-separated rows of gemmules, the lower row much the larger, the gemmules 10–11 to the whorl, close together, rising from defined spiral keels which override them as a sharp ridge, an extra row of gemmules on the base of the body whorl. Aperture simple, the outer margin straight, neither anterior spur nor posterior sinus discernible in the holotype. Columella column short, broad, and straight, a heavy ridge on its inner margin. Length of holotype 8·6 mm, if perfect probably 11 mm. Holotype, 11 paratypes, and numerous fragments.

Remarks.—This is the most attenuate of any of the Triphoridae seen, comparable only with *Triphoris asperrimus* Hinds from New Guinea. It is impossible from Hinds's description or figure to determine the characters of his species, but if Hedley's tentative identification of *asperrimus* from Funafuti is correct, it has different sculpture.

Genus VIRIOLA Jousseaume

Viriola oceanica, sp. nov.

Figs. 229 and 230

Shell of medium size, elongate, cylindrical in lower portion of spire, upper part conical, protoconch yellow-brown, remainder white. Protoconch conical, broad at base, tapering to an acute apex with slightly convex sides, nucleus small, domed, followed by 5 short whorls, the last 3 with double spiral keels crossed by fine axial cords. Mature whorls about 15, sutures not distinguishable. Sculpture 2 sharp, equal spiral keels, with a third small keel developing between them on the later whorls, the channels between with very faint axial threads, 2 extra small keels on the base of the body whorl. Aperture imperfect, showing neither the anterior spur nor posterior canal, but the columella column is long, oblique, and crossed by 2 small ribs. Length 7 mm. Holotype only.

Remarks.—This is close to *V. corrugata* Hinds, a species with a wide range in New Guinea and Queensland, but it is relatively broader, differs slightly in the sculpture, and has a different protoconch.

Genus MASTONIA Hinds

Mastonia anomala, sp. nov.

Figs. 231–233

Shell small, conical, slender for the genus, spire slightly convex, but not restricted at the base, protoconch brown, remainder cream. Protoconch relatively large, conical with a broad base, acuminate, of 7 short whorls with 2 strong, sharp spiral keels crossed by strong axial cords. Mature whorls 7, sutures not distinguishable. Sculpture 2 equal rows of large round gemmules, 14 to the whorl, with neither spiral nor axial connections, the body whorl with a small median row of gemmules and another on the base. Aperture round, expanded anteriorly but not tubular, the anterior spur not quite reaching the columella and sharply bent, posterior canal a round orifice connected by a slit with the outer margin. Columella column long, oblique, bent at the anterior end, crossed by several slight ribs, a heavy plate of callus on the inner margin. Length 3·8 mm. Holotype and three paratypes.

Remarks.—This is smaller than any other *Mastonia* studied, is narrower, and has fewer whorls than given in the generic description, but the sculpture, aperture, and protoconch are typical, and it may be considered a somewhat aberrant member of the genus.

Genus CORIOPHORA Laseron

Coriophora progressa, sp. nov.

Figs. 234–236

Shell of medium size, elongate, conical with convex sides, slightly restricted at the base, upper portion of spire white, remainder pale purple. Protoconch short, the true protoconch probably confined to the large, highly domed nucleus, the next 2 whorls with 2 prominent rounded spiral ribs, mature sculpture beginning gradually. Remaining whorls about 14, sutures not distinguishable. Sculpture of 2 equal rows of round gemmules, 20 to the whorl, about half their diameter apart, rising from ill-defined spiral keels and without axial connections, a small additional row on the base of the body whorl. Aperture round, subtubular, expanded anteriorly, entirely enclosing the anterior canal which opens within the aperture, posterior canal a circular orifice, connected by a narrow slit right on the suture with the outer margin. Columella column short, broad, and oblique, crossed by 2 narrow ribs, anteriorly truncate. Length 5·2 mm. Holotype and nine paratypes.

Remarks.—In form and colour this species most closely resembles *C. marceda* from northern Queensland and the Torres Strait, but differs in the protoconch, by having larger gemmules, and the aperture more advanced, approaching closely to the threefold stage.

Genus NANAPHORA Laseron

Nanaphora minuta, sp. nov.

Figs. 237 and 238

Shell minute, greatly inflated and restricted at the base, apex mammillate, colour of apex white, remainder cream, with yellow bands marking the spiral keels between the gemmules. Protoconch short, a small tilted nucleus followed by a large

inflated whorl, the next whorl with a single spiral keel. Mature whorls 6, the sutures not defined. Sculpture 2 equal rows of large round gemmules, 16 to the whorl, about half their diameter apart, rising from defined spiral keels, and connected axially by narrow ribs. On the body whorl the upper row of gemmules is larger, and there is an extra small row and 2 rounded smooth spiral keels on the rounded base. Aperture in the holotype probably not quite fully developed, as no posterior sinus is present and the anterior spur does not reach the columella. Columella pillar very short, rounded anteriorly. Length 2·4 mm. Holotype only.

Remarks.—This is amongst the smallest of all the species examined. It approaches nearest in form and sculpture to the type species *N. torquesa* previously described in Section V of this paper from Michaelmas Cay, but has a different colour pattern and particularly a different protoconch.

Genus OPIMAPHORA Laseron

Opimaphora coralina, sp. nov.

Figs. 239 and 240

Shell small, broad, medially inflated, acuminate above and restricted at the base, protoconch pale brown, remainder white with irregular brown patches, 2 of the paratypes wholly white. Protoconch relatively large, conical, and acuminate, of 6 whorls, nucleus small, next 3 whorls with single spiral keels, the final 2 with double keels overridden by strong axial cords. Mature whorls 6, sutures not distinct. Sculpture 2 equal rows of medium-sized round gemmules, 18 to the whorl, close together and rising from defined keels, no axial connections discernible, a small median row of gemmules developing on the later whorls. On the body whorl the rows of gemmules become progressively smaller anteriorly, with 2 extra rows and a smooth spiral keel on the rounded base. Aperture rounded, anterior spur just reaching the columella, posterior sinus shallow. Columella pillar short, broad, straight, rounded anteriorly, crossed by a low broad fold. Length 3 mm. Holotype and three paratypes.

Remarks.—The colour pattern and form is close to *O. sarcira* from the Capricorn Group, southern Queensland, and the sculpture resembles *O. litorea* from Darwin, but it differs from both in the aperture, and more particularly the protoconch.

Genus SUBULOPHORA Laseron

Subulophora indianica, sp. nov.

Figs. 241 and 242

Shell of medium size, attenuate, the spire with straight sides and only a slight taper, protoconch brown, remainder white. Protoconch conical, acuminate, tapering more rapidly than the spire, of 6 short whorls with 2 spiral keels close together and strong axial cords. Mature whorls 10, sutures well defined but not deep. Sculpture on the early whorls 2 rows of gemmules with a small row developing at the sutures in the later whorls, the body whorl with an extra row at the base, which is flattened. The gemmules of the lower row are larger, rounded, 14 to the whorl, and rise from defined spiral keels. Aperture polygonal, laterally expanded, the anterior spur not

quite reaching the columella, posterior canal a deep slit right on the suture. Columella pillar short, broad, and straight, rounded anteriorly, a callus on the inner margin. Length 5·5 mm. Holotype and two paratypes.

Remarks.—In form and sculpture this is a typical *Subulophora*, approaching closely to the type species *S. stringera*, but it differs in details of the aperture and sculpture, and by having two spiral keels on the protoconch instead of one.

Subulophora virgina, sp. nov.

Figs. 243 and 244

Shell small, attenuate, spire with straight sides and little taper, white. Protoconch conical, acuminate, in line of spire, of 6 whorls, with a single spiral keel crossed by fine axial threads. Mature whorls 10, parted by deep sutures. Sculpture on the early whorls 2 nearly equal rows of small gemmules, with a third smaller median row developing on the later whorls, and attaining the same size as the others on the penultimate whorl, the body whorl with an extra nearly smooth spiral keel on the flattened base. The gemmules are small, 18 to the whorl, about their own diameter apart, and rise above defined spiral keels but with no apparent axial connections. Aperture simple, the outer margin straight, the anterior spur not reaching the columella, the posterior canal a V-shaped notch right on the suture. Columella column nearly straight, anterior margin obliquely truncate, a thick plate of callus on the inner margin. Length 4 mm. Holotype and four paratypes.

Remarks.—By the deep sutures this species generally resembles *S. minima* from Darwin, but differs chiefly by the smaller and more numerous gemmules.

Subulophora marginata, sp. nov.

Figs. 245 and 246

Shell of medium size, elongate, lower portion of spire cylindrical, upper part conical and slightly convex, protoconch brown, remainder yellowish white with a pale brown band marking the spiral keels between the gemmules. Protoconch conical and acuminate, of 5 whorls, with a double spiral keel and fine axial threads, mature sculpture beginning abruptly. Mature whorls 14, sutures not distinct. Sculpture on the early whorls 2 nearly equal rows of medium-sized rounded gemmules, 16 to the whorl, rather more than half their diameter apart, rising from defined spiral keels, with a third small row of gemmules developing on the later whorls just below the suture, with 2 nearly smooth spiral keels in addition on the rounded base of the body whorl. Aperture simple, the outer margin straight, the anterior spur sharply bent and not quite reaching the columella, posterior sinus not apparent in the holotype, but may be broken. Columella column nearly straight, tapering anteriorly, crossed by a broad rib near its base, a heavy plate of callus on the inner margin. Length 5·4 mm. Holotype only.

Remarks.—The form and particularly the sculpture, with the small row of gemmules adjacent to and just below the suture, distinguish this species from the others here discussed. The colour band between the gemmules, though faint, is also a good recognition feature.

VII. New Genera

New genera proposed in the present paper are *Aclophora*, *Contraforis*, *Coriophora*, *Distophora*, *Epiforis*, *Liniphora*, *Mesophora*, *Nanaphora*, *Opimaphora*, *Orbitophora*, *Subulophora*, *Tetraphora*, and *Torresophora*.

VIII. Acknowledgments

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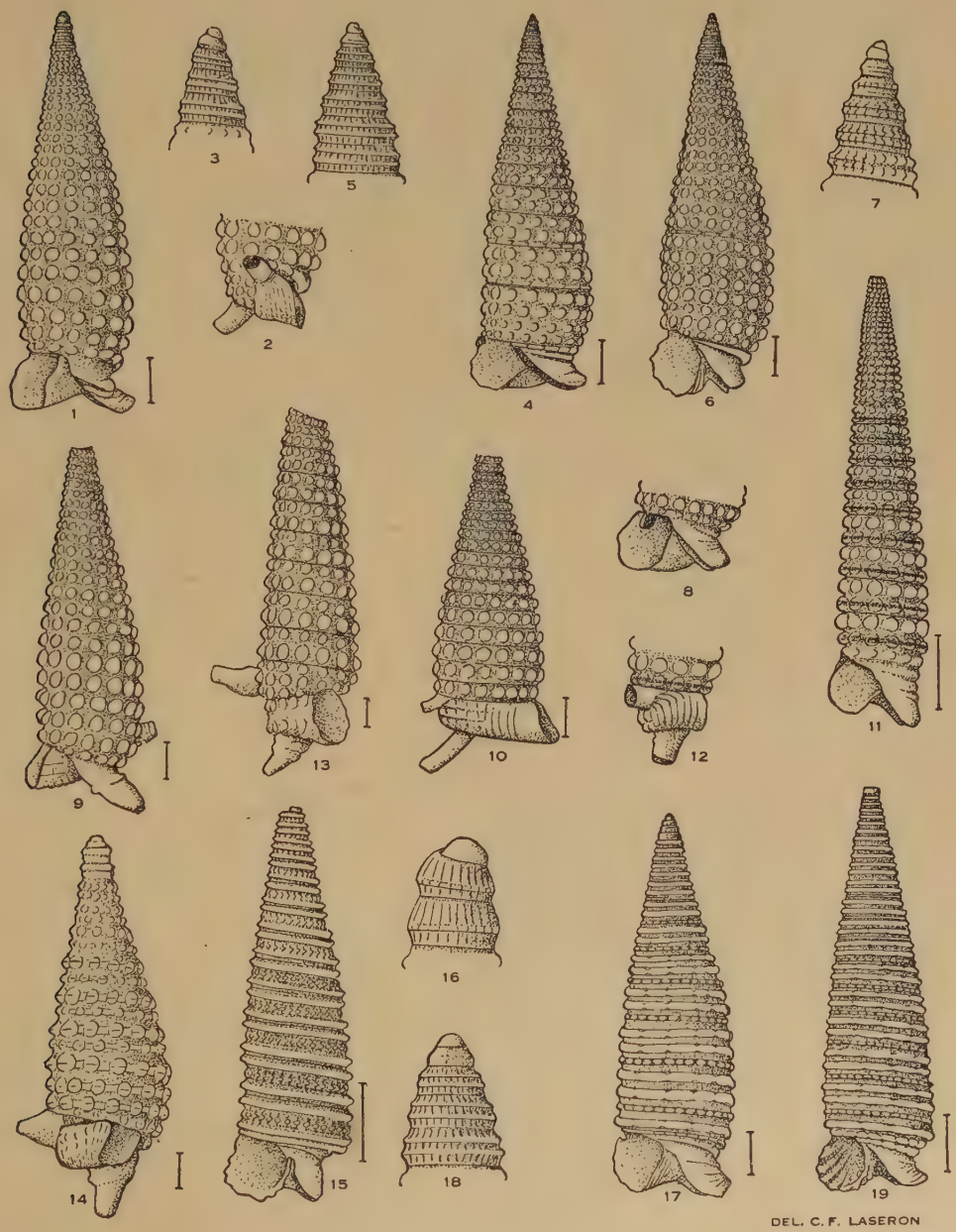

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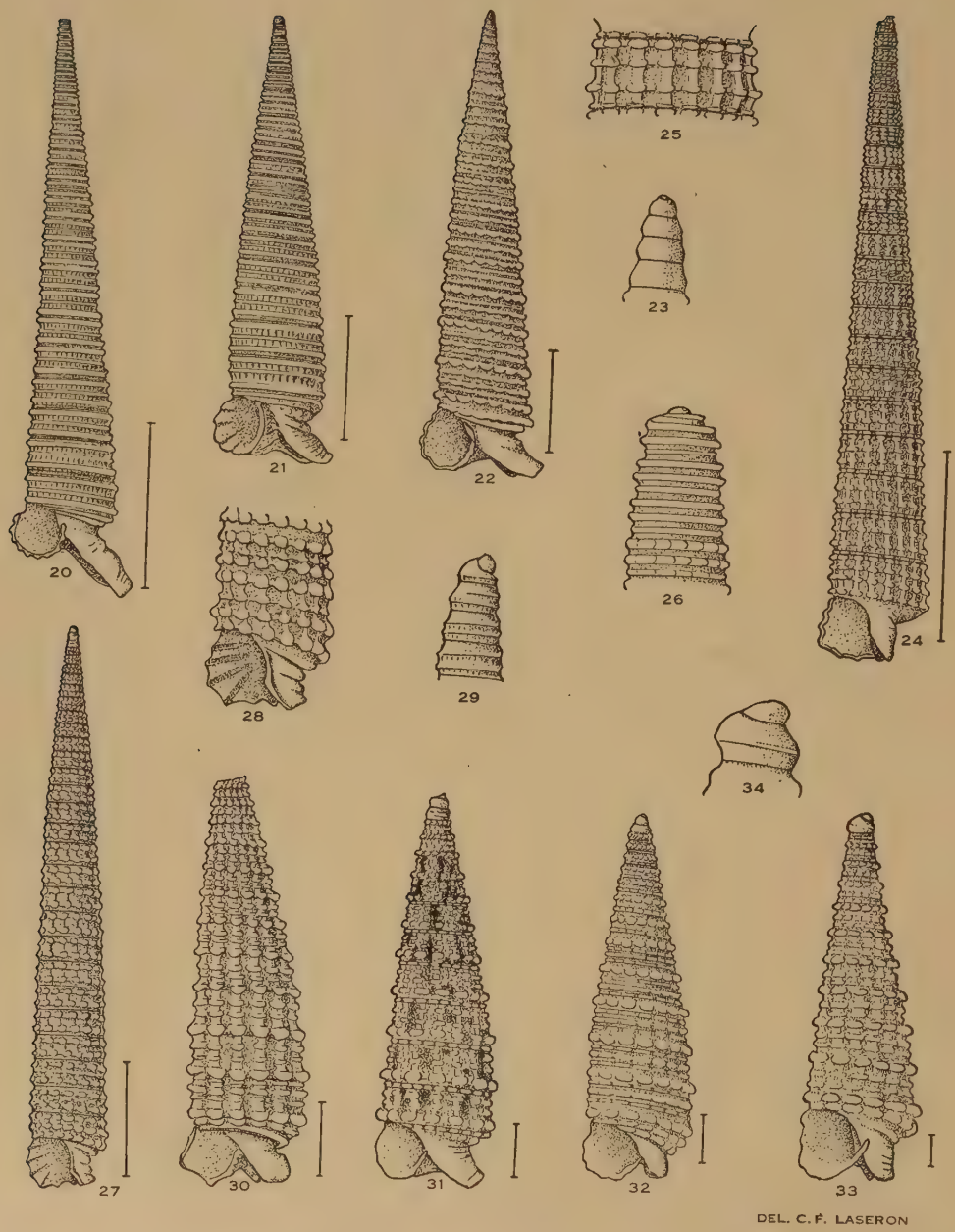

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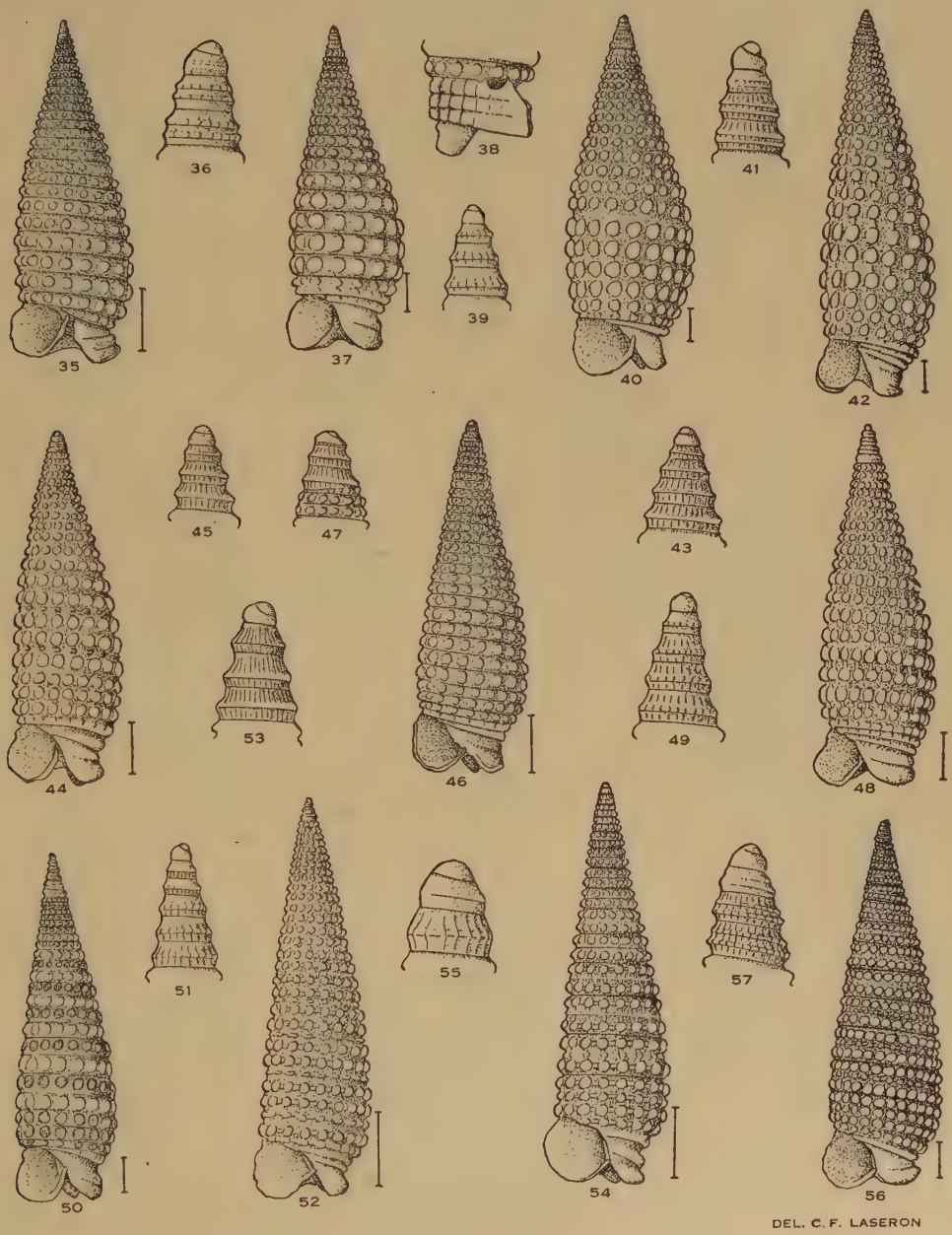

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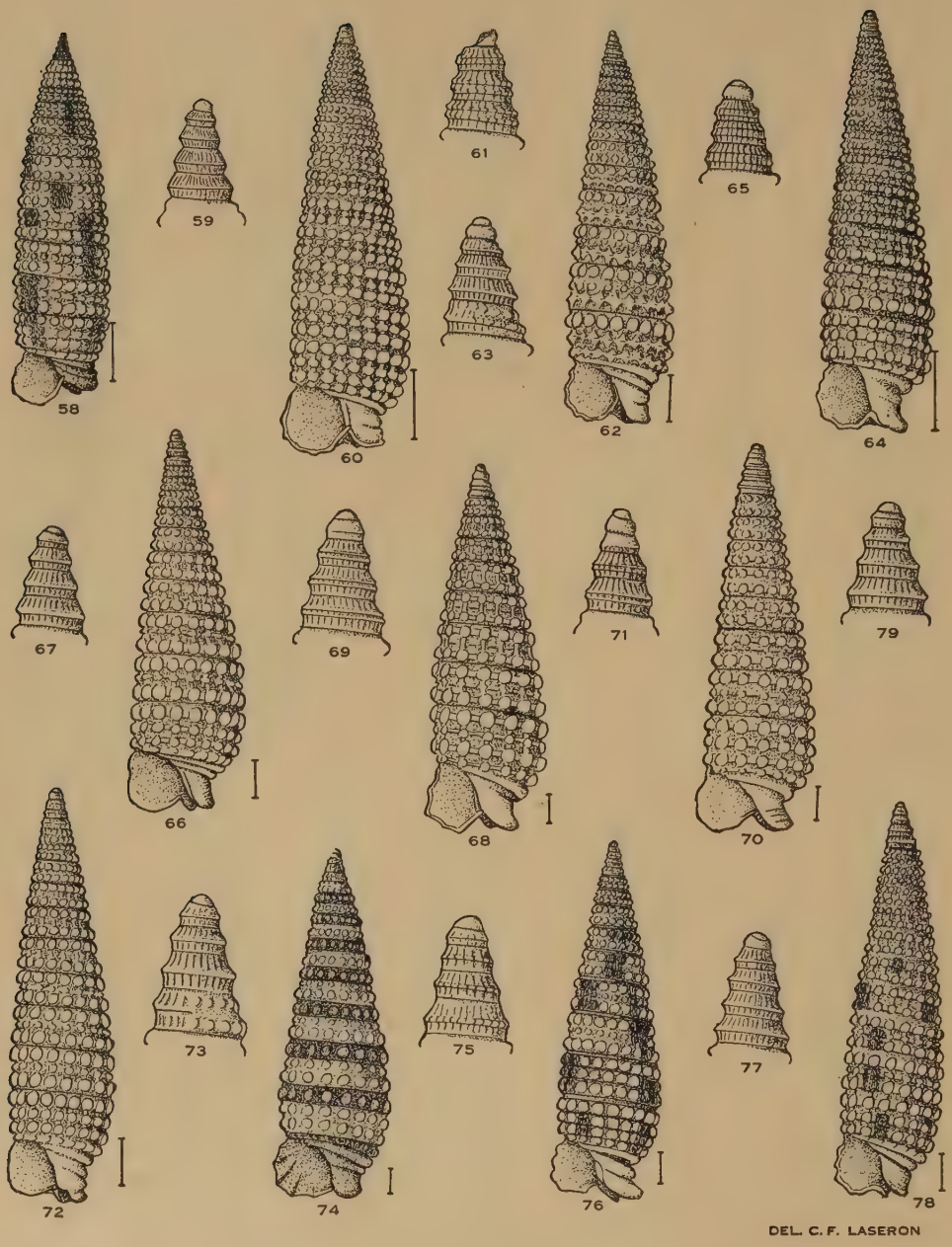

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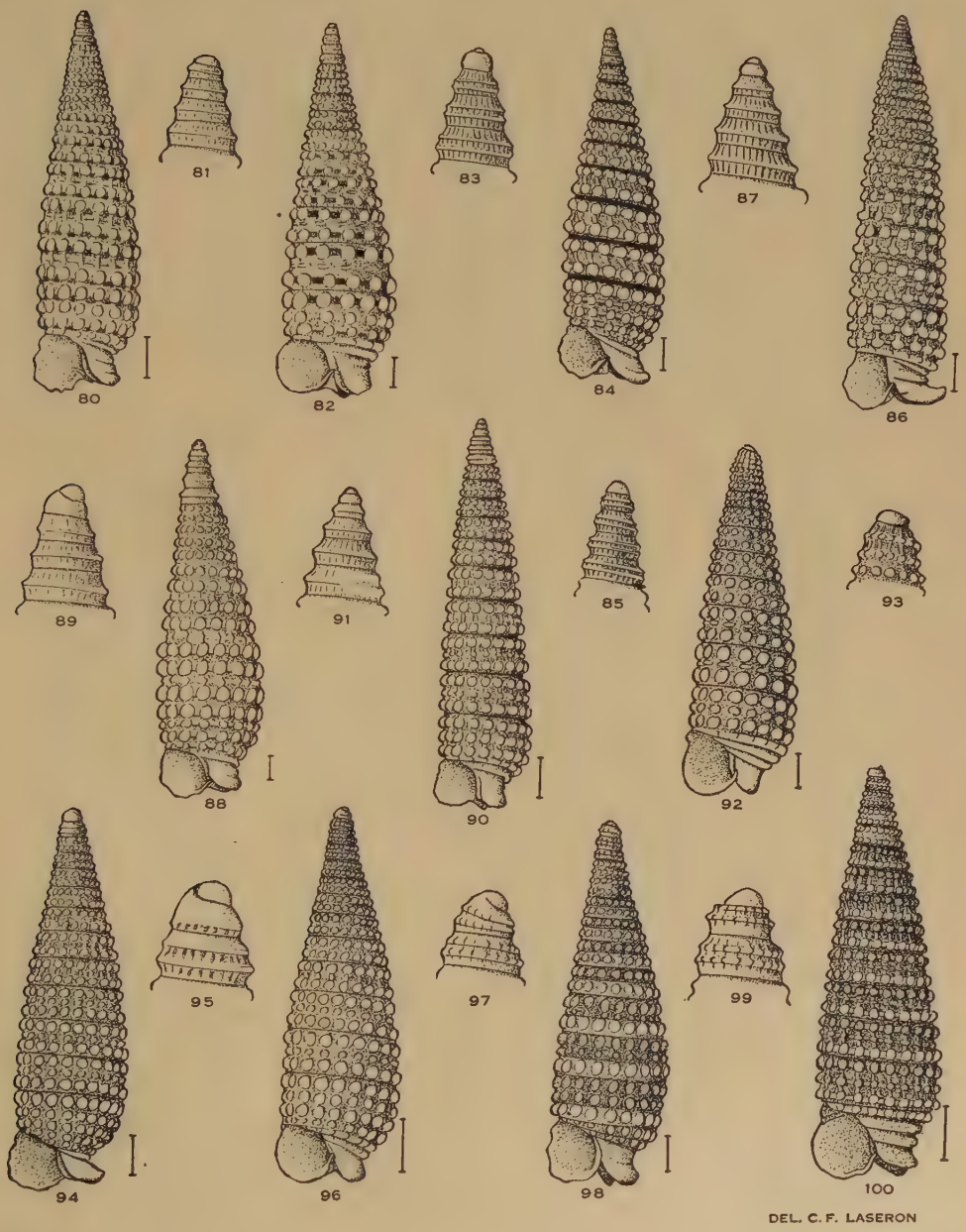

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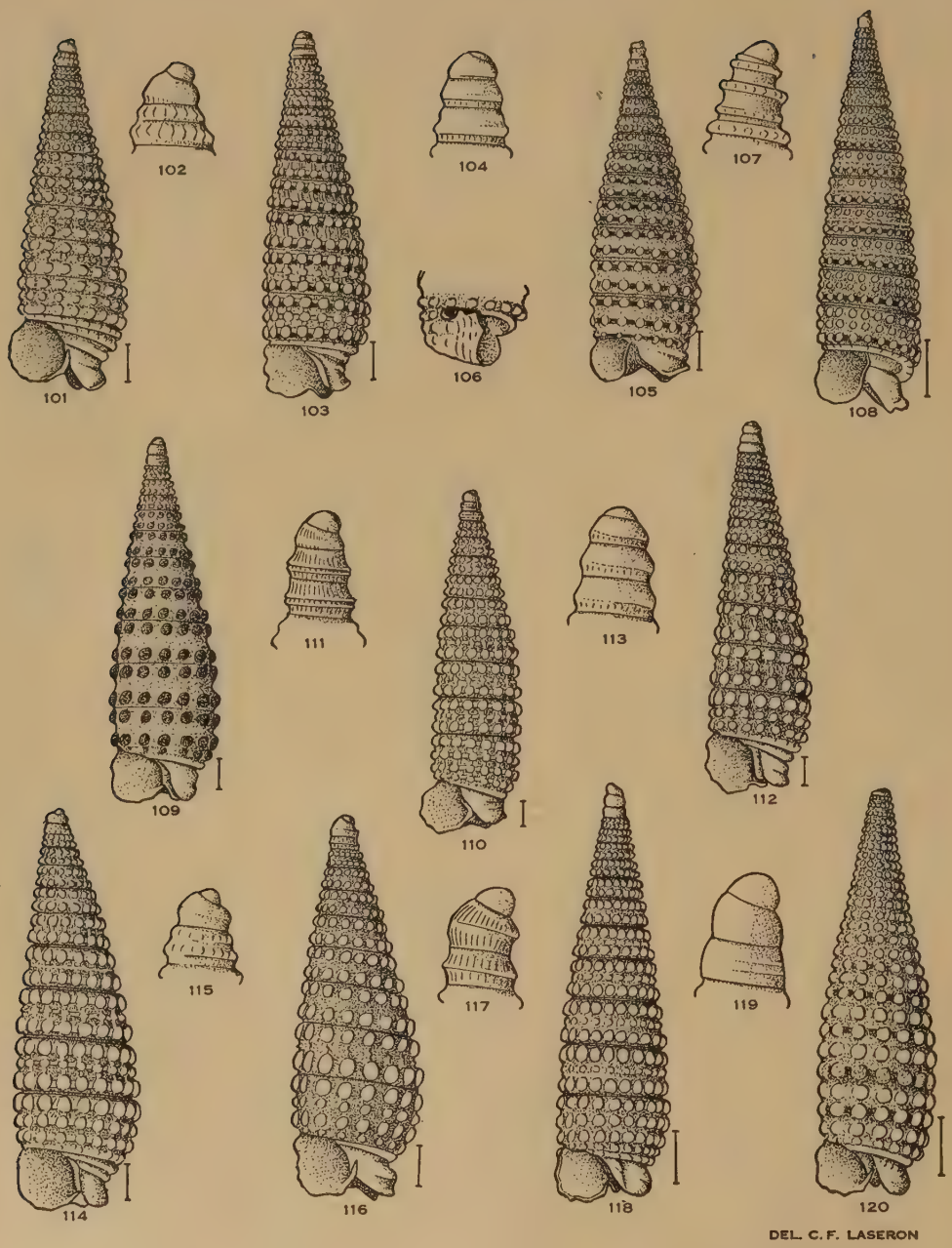

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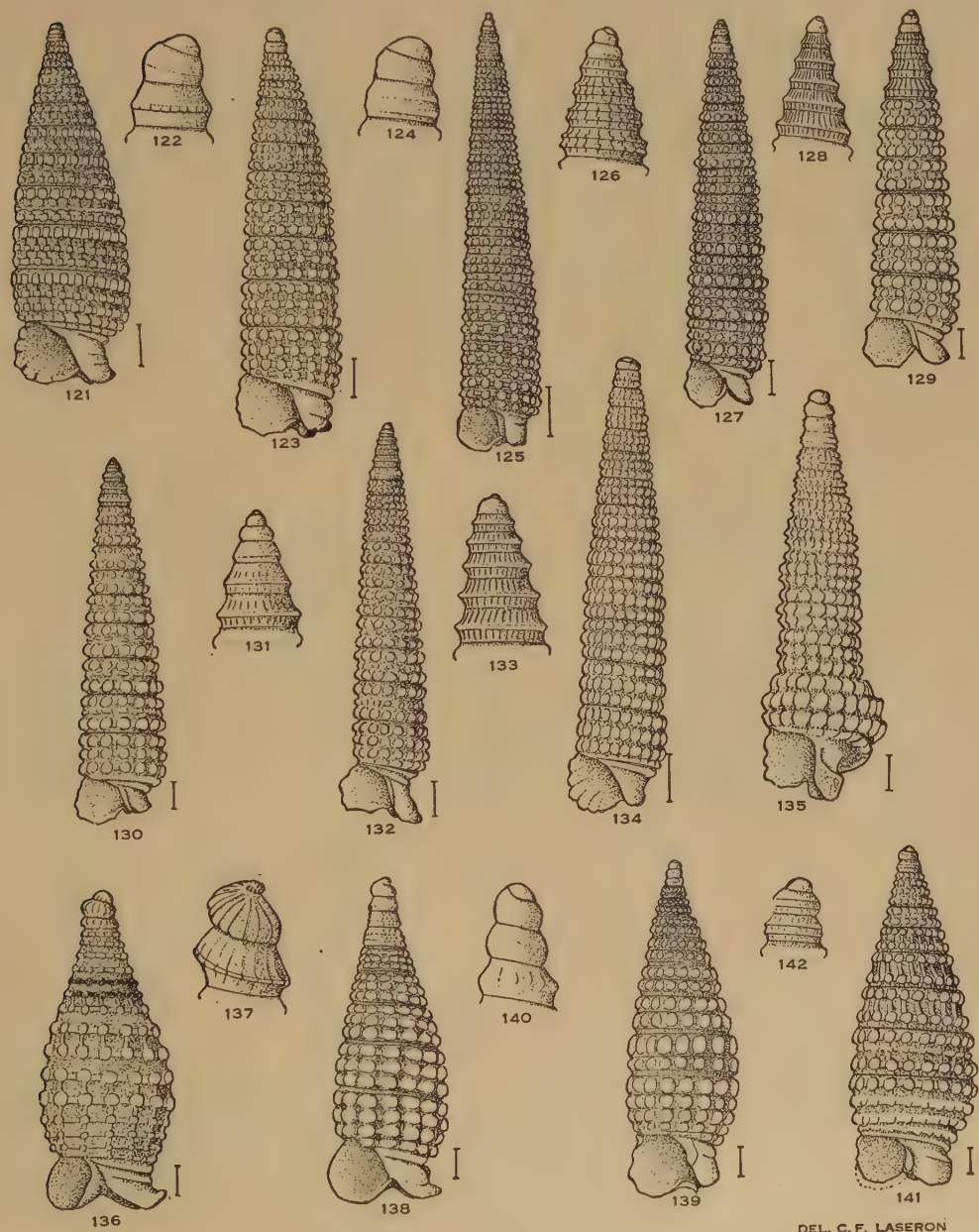

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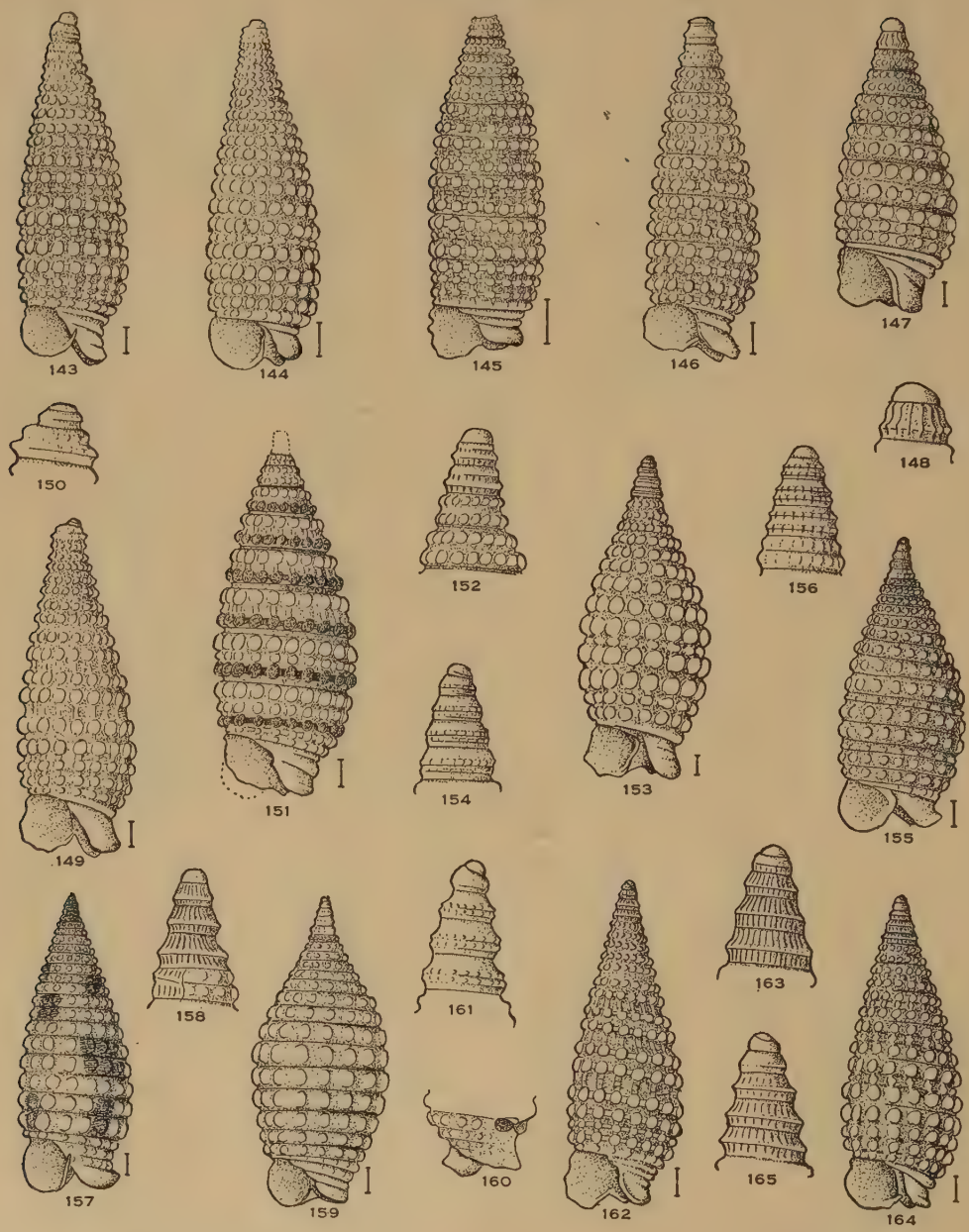

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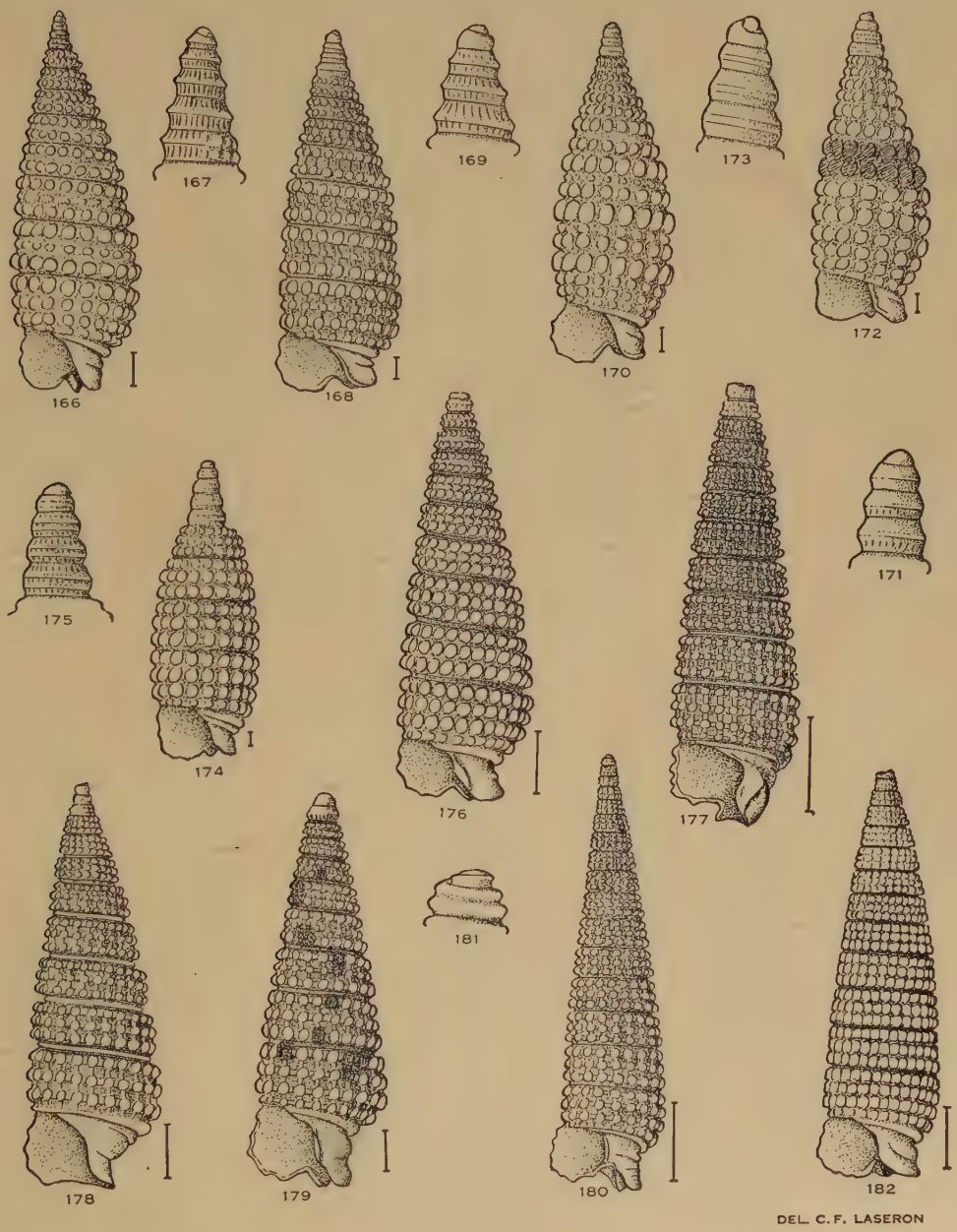

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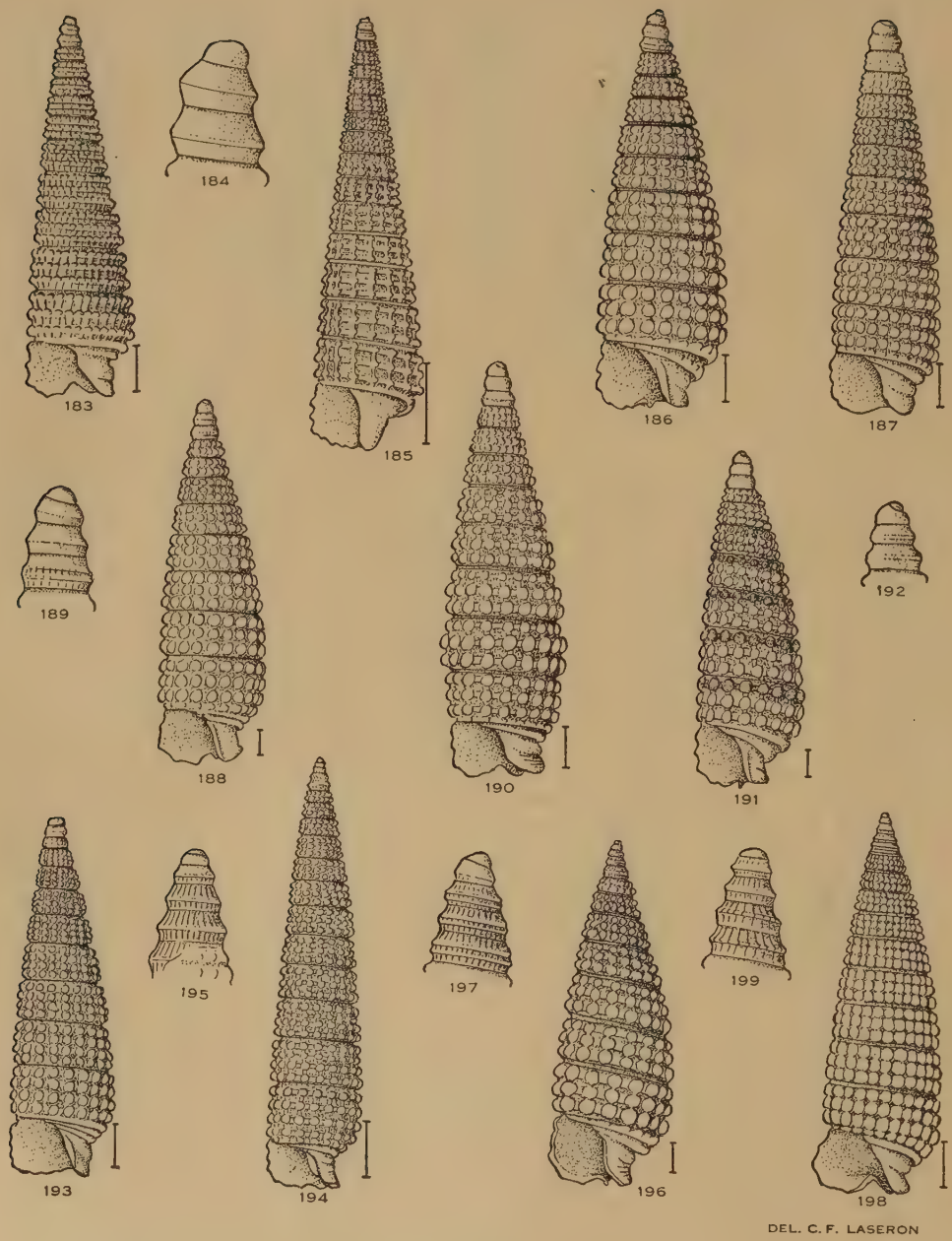

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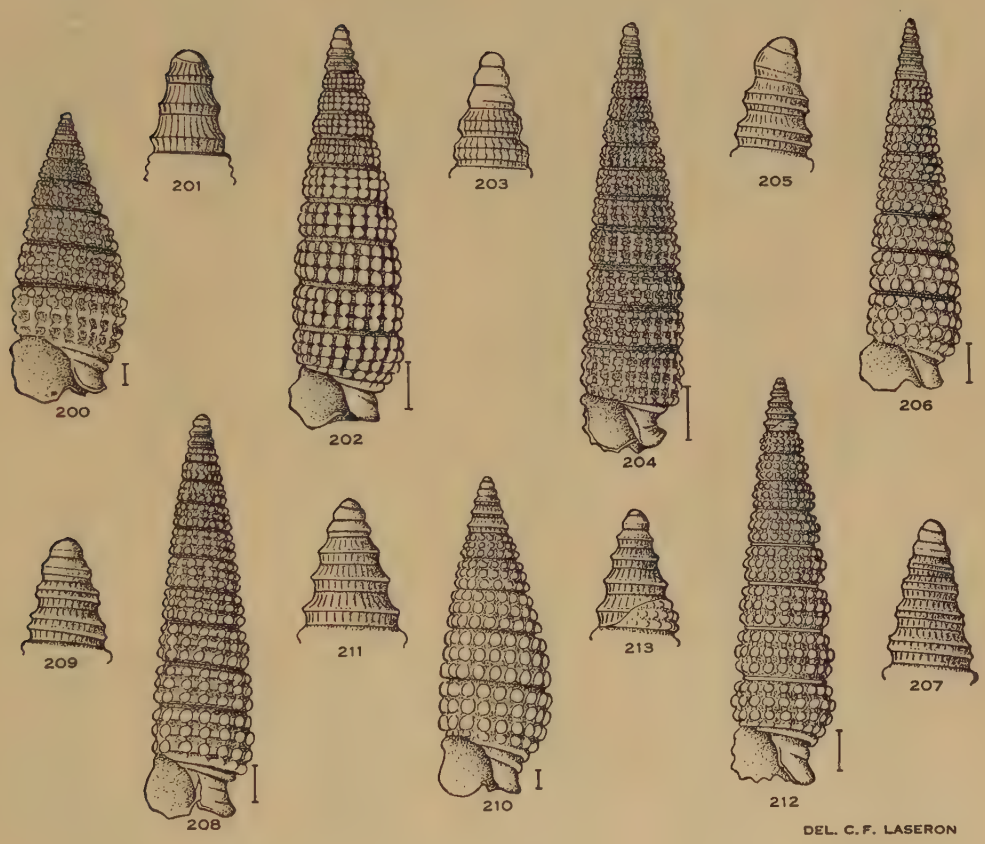

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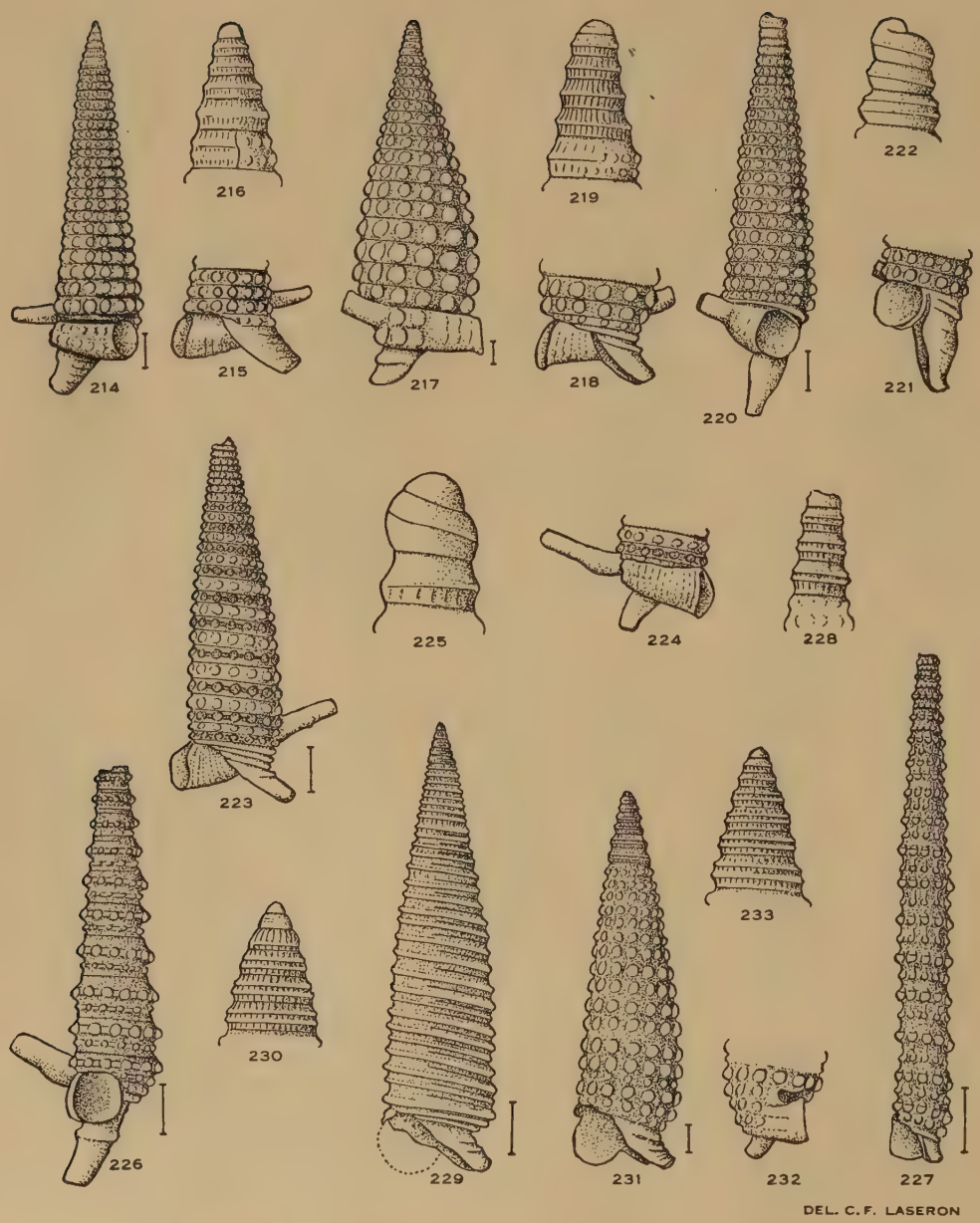

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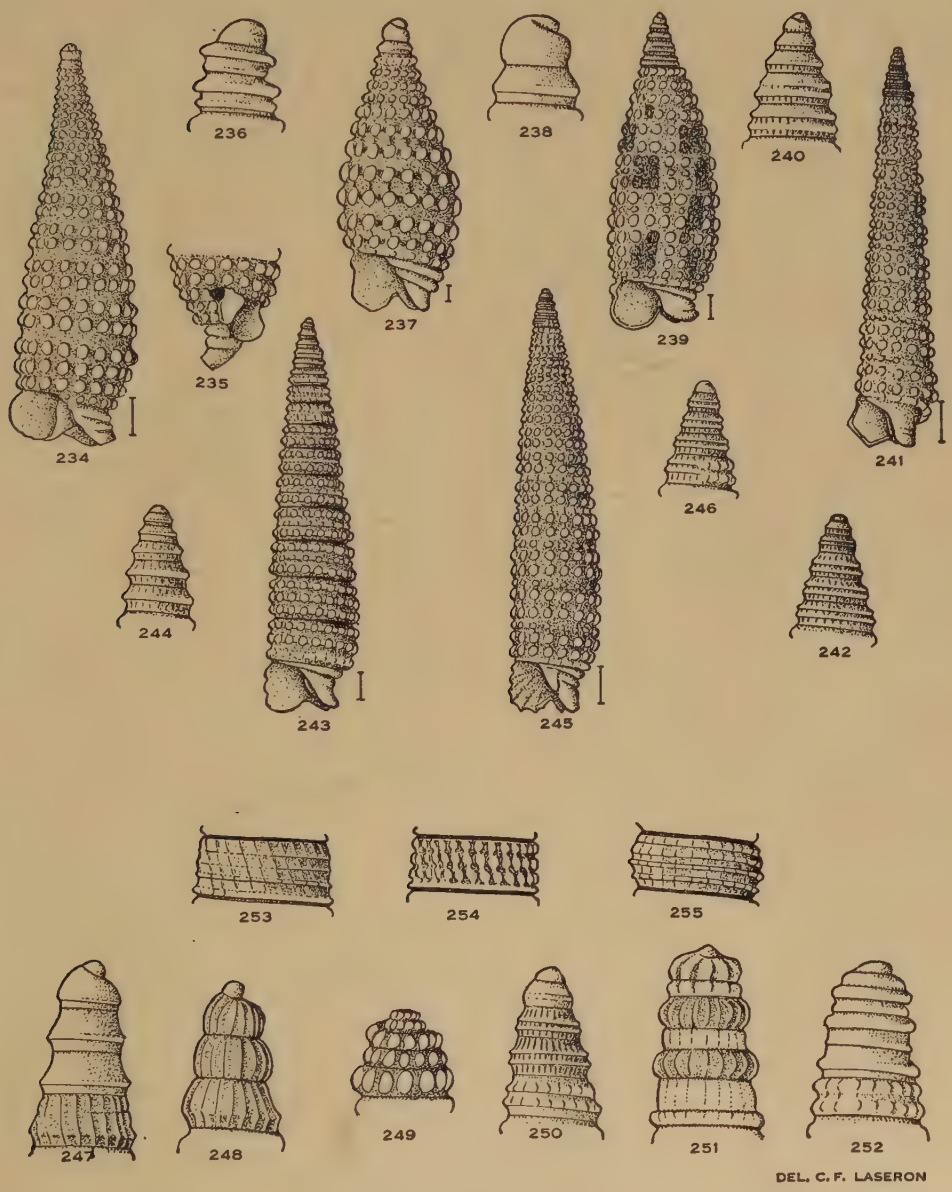

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